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The Plant Body

By the end of this section, you will be able to:

- Describe the shoot organ system and the root organ system
- Distinguish between meristematic tissue and permanent tissue
- Identify and describe the three regions where plant growth occurs
- Summarize the roles of dermal tissue, vascular tissue, and ground tissue
- Compare simple plant tissue with complex plant tissue

Like animals, plants contain cells with organelles in which specific metabolic activities take place.

Unlike animals, however, plants use energy from sunlight to form sugars during photosynthesis. In addition, plant cells have cell walls, plastids, and a large central vacuole: structures that are not found in animal cells. Each of these cellular structures plays a specific role in plant structure and function.

Link to Learning



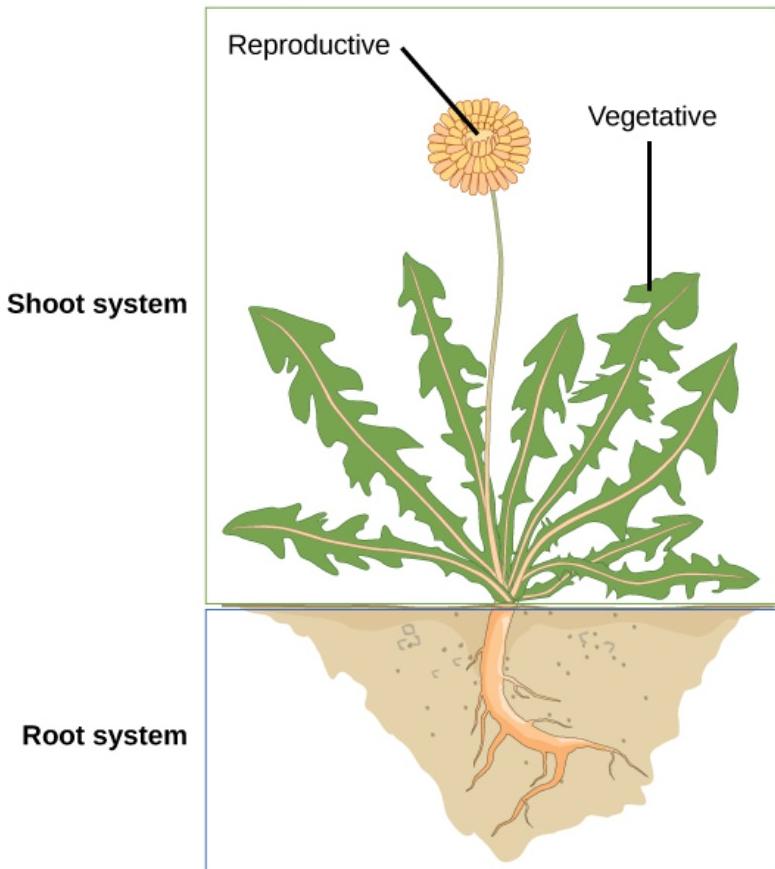
Watch *Botany Without Borders*, a video produced by the Botanical Society of America about the importance of plants.

The shoot system of a plant consists of leaves, stems, flowers, and fruits. The root system anchors the plant while absorbing water and minerals from the soil.

Plant Organ Systems

In plants, just as in animals, similar cells working together form a tissue. When different types of tissues work together to perform a unique function, they form an organ; organs working together form organ systems. Vascular plants have two distinct organ systems: a shoot system, and a root system. The **shoot system** consists of two portions: the vegetative (non-reproductive) parts of the plant, such as the leaves and the stems, and the reproductive parts of the plant, which include flowers and fruits. The shoot system generally grows above ground, where it absorbs the light needed for

photosynthesis. The **root system**, which supports the plants and absorbs water and minerals, is usually underground. [\[link\]](#) shows the organ systems of a typical plant.



This light micrograph shows a cross section of a squash (*Cucurbita maxima*) stem. Each teardrop-shaped vascular bundle consists of large xylem vessels toward the inside and smaller phloem cells toward the outside. Xylem cells, which transport water and nutrients from the roots to the rest of the plant, are dead at functional maturity. Phloem cells, which transport sugars and other organic

compounds from photosynthetic tissue to the rest of the plant, are living. The vascular bundles are encased in ground tissue and surrounded by dermal tissue. (credit: modification of work by "(biophotos)"/Flickr; scale-bar data from Matt Russell)

Plant Tissues

Plants are multicellular eukaryotes with tissue systems made of various cell types that carry out specific functions. Plant tissue systems fall into one of two general types: meristematic tissue, and permanent (or non-meristematic) tissue. Cells of the meristematic tissue are found in **meristems**, which are plant regions of continuous cell division and growth. **Meristematic tissue** cells are either undifferentiated or incompletely differentiated, and they continue to divide and contribute to the growth of the plant. In contrast, **permanent tissue** consists of plant cells that are no longer actively dividing.

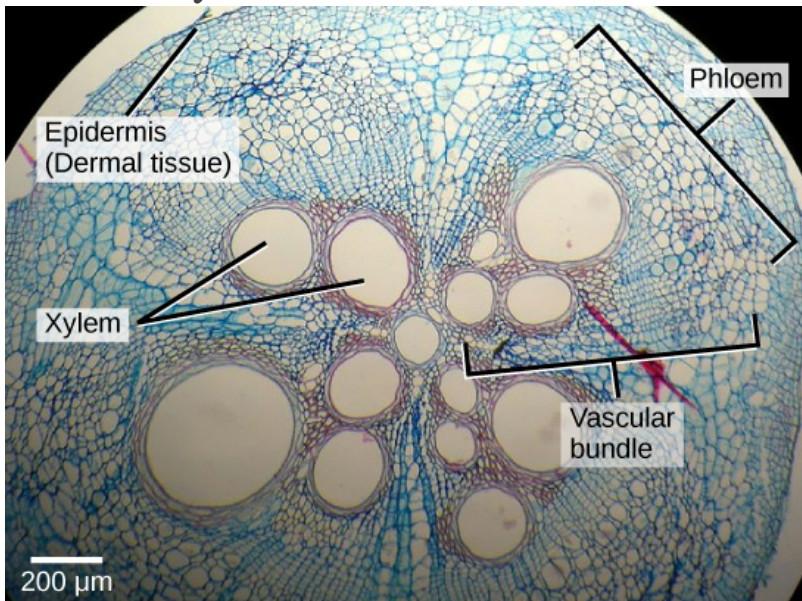
Meristematic tissues consist of three types, based on their location in the plant. **Apical meristems** contain meristematic tissue located at the tips of stems and roots, which enable a plant to extend in length. **Lateral meristems** facilitate growth in thickness or girth in a maturing plant. **Intercalary meristems** occur only in monocots, at the bases of leaf blades and at nodes (the areas where leaves attach to a stem). This tissue enables the monocot

leaf blade to increase in length from the leaf base; for example, it allows lawn grass leaves to elongate even after repeated mowing.

Meristems produce cells that quickly differentiate, or specialize, and become permanent tissue. Such cells take on specific roles and lose their ability to divide further. They differentiate into three main types: dermal, vascular, and ground tissue. **Dermal tissue** covers and protects the plant, and **vascular tissue** transports water, minerals, and sugars to different parts of the plant. **Ground tissue** serves as a site for photosynthesis, provides a supporting matrix for the vascular tissue, and helps to store water and sugars.

Secondary tissues are either simple (composed of similar cell types) or complex (composed of different cell types). Dermal tissue, for example, is a simple tissue that covers the outer surface of the plant and controls gas exchange. Vascular tissue is an example of a complex tissue, and is made of two specialized conducting tissues: xylem and phloem. Xylem tissue transports water and nutrients from the roots to different parts of the plant, and includes three different cell types: vessel elements and tracheids (both of which conduct water), and xylem parenchyma. Phloem tissue, which transports organic compounds from the site of photosynthesis to other parts of the plant, consists of four different cell types: sieve cells (which conduct

photosynthates), companion cells, phloem parenchyma, and phloem fibers. Unlike xylem conducting cells, phloem conducting cells are alive at maturity. The xylem and phloem always lie adjacent to each other ([\[link\]](#)). In stems, the xylem and the phloem form a structure called a **vascular bundle**; in roots, this is termed the **vascular stele** or **vascular cylinder**.



Section Summary

A vascular plant consists of two organ systems: the shoot system and the root system. The shoot system includes the aboveground vegetative portions (stems and leaves) and reproductive parts (flowers and fruits). The root system supports the plant and is

usually underground. A plant is composed of two main types of tissue: meristematic tissue and permanent tissue. Meristematic tissue consists of actively dividing cells found in root and shoot tips. As growth occurs, meristematic tissue differentiates into permanent tissue, which is categorized as either simple or complex. Simple tissues are made up of similar cell types; examples include dermal tissue and ground tissue. Dermal tissue provides the outer covering of the plant. Ground tissue is responsible for photosynthesis; it also supports vascular tissue and may store water and sugars. Complex tissues are made up of different cell types. Vascular tissue, for example, is made up of xylem and phloem cells.

Review Questions

Plant regions of continuous growth are made up of _____.

1. dermal tissue
2. vascular tissue
3. meristematic tissue
4. permanent tissue

Which of the following is the major site of photosynthesis?

1. apical meristem
 2. ground tissue
 3. xylem cells
 4. phloem cells
-

B

Free Response

What type of meristem is found only in monocots, such as lawn grasses? Explain how this type of meristematic tissue is beneficial in lawn grasses that are mowed each week.

Lawn grasses and other monocots have an intercalary meristem, which is a region of meristematic tissue at the base of the leaf blade. This is beneficial to the plant because it can continue to grow even when the tip of the plant is removed by grazing or mowing.

Which plant part is responsible for transporting

water, minerals, and sugars to different parts of the plant? Name the two types of tissue that make up this overall tissue, and explain the role of each.

Vascular tissue transports water, minerals, and sugars throughout the plant. Vascular tissue is made up of xylem tissue and phloem tissue. Xylem tissue transports water and nutrients from the roots upward. Phloem tissue carries sugars from the sites of photosynthesis to the rest of the plant.

Glossary

apical meristem

meristematic tissue located at the tips of stems and roots; enables a plant to extend in length

dermal tissue

protective plant tissue covering the outermost part of the plant; controls gas exchange

ground tissue

plant tissue involved in photosynthesis; provides support, and stores water and sugars

intercalary meristem

meristematic tissue located at nodes and the

bases of leaf blades; found only in monocots

lateral meristem

meristematic tissue that enables a plant to increase in thickness or girth

meristematic tissue

tissue containing cells that constantly divide; contributes to plant growth

meristem

plant region of continuous growth

permanent tissue

plant tissue composed of cells that are no longer actively dividing

root system

belowground portion of the plant that supports the plant and absorbs water and minerals

shoot system

aboveground portion of the plant; consists of non-reproductive plant parts, such as leaves and stems, and reproductive parts, such as flowers and fruits

vascular bundle

strands of stem tissue made up of xylem and phloem

vascular stele

strands of root tissue made up of xylem and phloem

vascular tissue

tissue made up of xylem and phloem that transports food and water throughout the plant

Stems

By the end of this section, you will be able to:

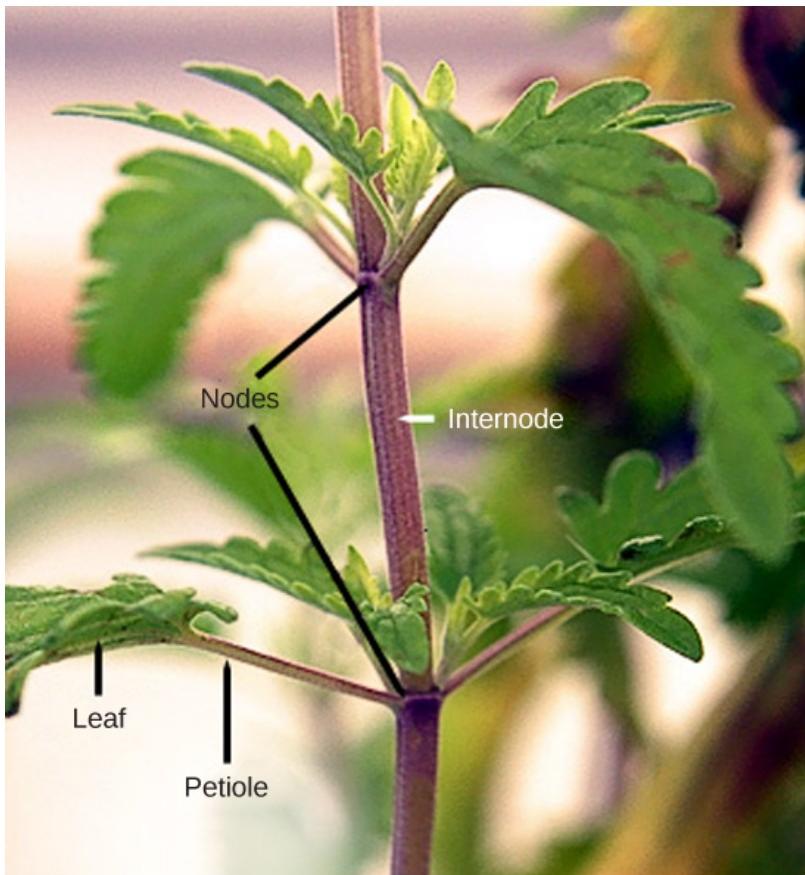
- Describe the main function and basic structure of stems
- Compare and contrast the roles of dermal tissue, vascular tissue, and ground tissue
- Distinguish between primary growth and secondary growth in stems
- Summarize the origin of annual rings
- List and describe examples of modified stems

Stems are a part of the shoot system of a plant. They may range in length from a few millimeters to hundreds of meters, and also vary in diameter, depending on the plant type. Stems are usually above ground, although the stems of some plants, such as the potato, also grow underground. Stems may be herbaceous (soft) or woody in nature. Their main function is to provide support to the plant, holding leaves, flowers and buds; in some cases, stems also store food for the plant. A stem may be unbranched, like that of a palm tree, or it may be highly branched, like that of a magnolia tree. The stem of the plant connects the roots to the leaves, helping to transport absorbed water and minerals to different parts of the plant. It also helps to transport the products of photosynthesis, namely sugars, from the leaves to the rest of the plant.

Plant stems, whether above or below ground, are

characterized by the presence of nodes and internodes ([\[link\]](#)). **Nodes** are points of attachment for leaves, aerial roots, and flowers. The stem region between two nodes is called an **internode**. The stalk that extends from the stem to the base of the leaf is the petiole. An **axillary bud** is usually found in the axil—the area between the base of a leaf and the stem—where it can give rise to a branch or a flower. The apex (tip) of the shoot contains the apical meristem within the **apical bud**.

Leaves are attached to the plant stem at areas called nodes. An internode is the stem region between two nodes. The petiole is the stalk connecting the leaf to the stem. The leaves just above the nodes arose from axillary buds.



The stem of common St John's Wort (*Hypericum perforatum*) is shown in cross section in this light micrograph. The central pith (greenish-blue, in the center) and peripheral cortex (narrow zone 3–5 cells thick just inside the epidermis) are composed of parenchyma cells. Vascular tissue composed of xylem (red) and phloem tissue (green, between the xylem and cortex) surrounds the pith. (credit: Rolf-Dieter Mueller) Collenchyma cell walls are uneven in thickness, as seen in this light micrograph. They provide support to plant structures. (credit: modification of work by Carl Szczerski; scale-bar

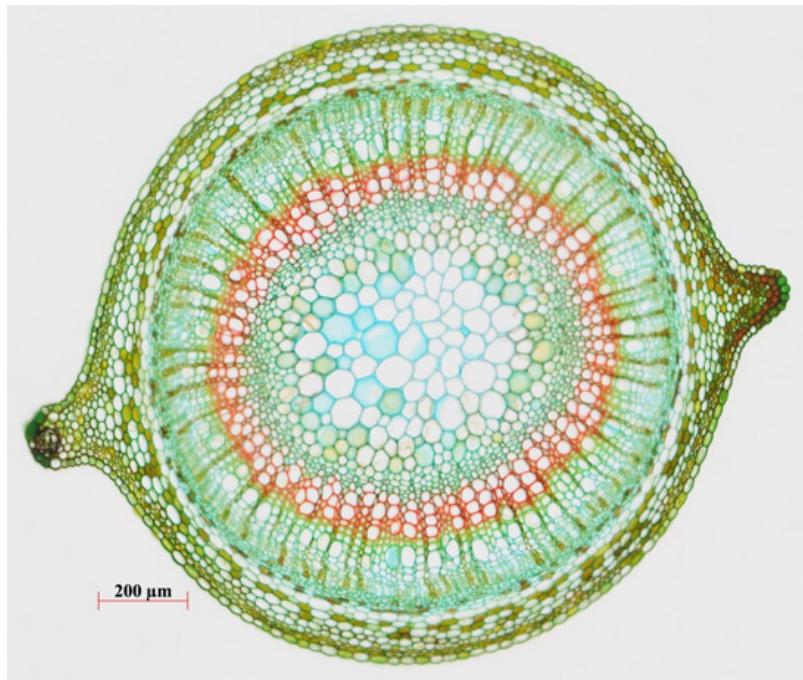
data from Matt Russell) Openings called stomata (singular: stoma) allow a plant to take up carbon dioxide and release oxygen and water vapor. The (a) colorized scanning-electron micrograph shows a closed stoma of a dicot. Each stoma is flanked by two guard cells that regulate its (b) opening and closing. The (c) guard cells sit within the layer of epidermal cells (credit a: modification of work by Louisa Howard, Rippel Electron Microscope Facility, Dartmouth College; credit b: modification of work by June Kwak, University of Maryland; scale-bar data from Matt Russell) In (a) dicot stems, vascular bundles are arranged around the periphery of the ground tissue. The xylem tissue is located toward the interior of the vascular bundle, and phloem is located toward the exterior. Sclerenchyma fibers cap the vascular bundles. In (b) monocot stems, vascular bundles composed of xylem and phloem tissues are scattered throughout the ground tissue.

Stem Anatomy

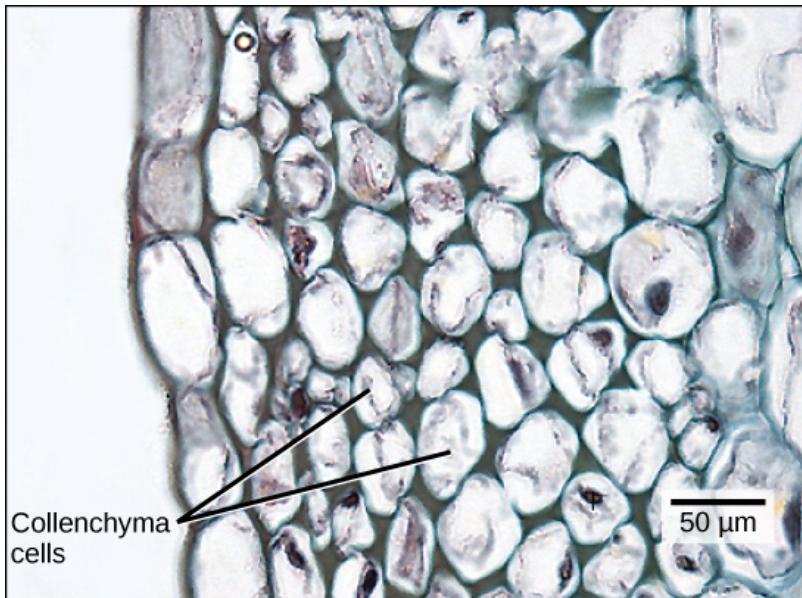
The stem and other plant organs arise from the ground tissue, and are primarily made up of simple tissues formed from three types of cells: parenchyma, collenchyma, and sclerenchyma cells.

Parenchyma cells are the most common plant cells ([\[link\]](#)). They are found in the stem, the root, the inside of the leaf, and the pulp of the fruit. Parenchyma cells are responsible for metabolic

functions, such as photosynthesis, and they help repair and heal wounds. Some parenchyma cells also store starch.



Collenchyma cells are elongated cells with unevenly thickened walls ([\[link\]](#)). They provide structural support, mainly to the stem and leaves. These cells are alive at maturity and are usually found below the epidermis. The “strings” of a celery stalk are an example of collenchyma cells.

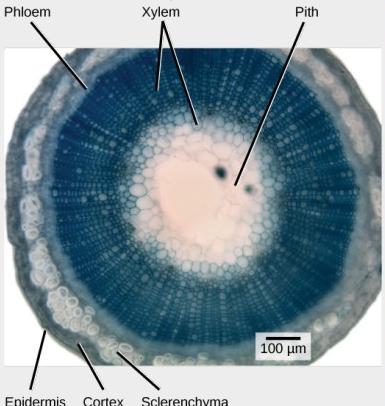


Sclerenchyma cells also provide support to the plant, but unlike collenchyma cells, many of them are dead at maturity. There are two types of sclerenchyma cells: fibers and sclereids. Both types have secondary cell walls that are thickened with deposits of lignin, an organic compound that is a key component of wood. Fibers are long, slender cells; sclereids are smaller-sized. Sclereids give pears their gritty texture. Humans use sclerenchyma fibers to make linen and rope ([\[link\]](#)).

Art Connection

The central pith and outer cortex of the (a) flax stem are made up of parenchyma cells. Inside the cortex is a layer of sclerenchyma cells, which make

up the fibers in flax rope and clothing. Humans have grown and harvested flax for thousands of years. In (b) this drawing, fourteenth-century women prepare linen. The (c) flax plant is grown and harvested for its fibers, which are used to weave linen, and for its seeds, which are the source of linseed oil. (credit a: modification of work by Emmanuel Boutet based on original work by Ryan R. MacKenzie; credit c: modification of work by Brian Dearth; scale-bar data from Matt Russell)



(a)



(b)



(c)

Which layers of the stem are made of parenchyma cells?

1. cortex and pith
2. phloem

3. sclerenchyma

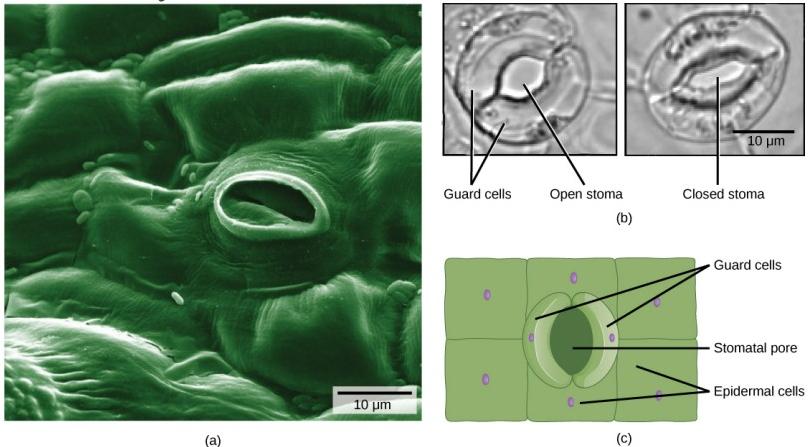
4. xylem

Like the rest of the plant, the stem has three tissue systems: dermal, vascular, and ground tissue. Each is distinguished by characteristic cell types that perform specific tasks necessary for the plant's growth and survival.

Dermal Tissue

The dermal tissue of the stem consists primarily of **epidermis**, a single layer of cells covering and protecting the underlying tissue. Woody plants have a tough, waterproof outer layer of cork cells commonly known as **bark**, which further protects the plant from damage. Epidermal cells are the most numerous and least differentiated of the cells in the epidermis. The epidermis of a leaf also contains openings known as stomata, through which the exchange of gases takes place ([\[link\]](#)). Two cells, known as **guard cells**, surround each leaf stoma, controlling its opening and closing and thus regulating the uptake of carbon dioxide and the release of oxygen and water vapor. **Trichomes** are hair-like structures on the epidermal surface. They help to reduce **transpiration** (the loss of water by aboveground plant parts), increase solar reflectance, and store compounds that defend the leaves against

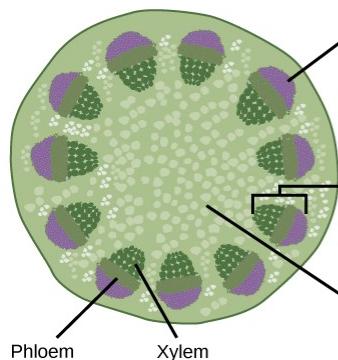
predation by herbivores.



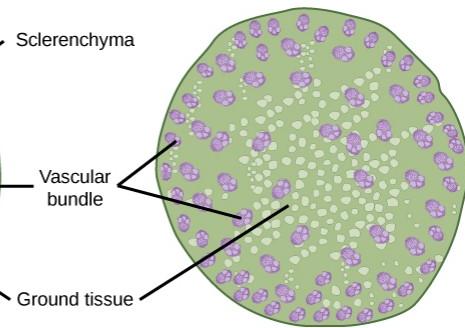
Vascular Tissue

The xylem and phloem that make up the vascular tissue of the stem are arranged in distinct strands called vascular bundles, which run up and down the length of the stem. When the stem is viewed in cross section, the vascular bundles of dicot stems are arranged in a ring. In plants with stems that live for more than one year, the individual bundles grow together and produce the characteristic growth rings. In monocot stems, the vascular bundles are randomly scattered throughout the ground tissue ([\[link\]](#)).

Dicot stem



Monocot stem



Xylem tissue has three types of cells: xylem parenchyma, tracheids, and vessel elements. The latter two types conduct water and are dead at maturity. **Tracheids** are xylem cells with thick secondary cell walls that are lignified. Water moves from one tracheid to another through regions on the side walls known as pits, where secondary walls are absent. **Vessel elements** are xylem cells with thinner walls; they are shorter than tracheids. Each vessel element is connected to the next by means of a perforation plate at the end walls of the element. Water moves through the perforation plates to travel up the plant.

Phloem tissue is composed of sieve-tube cells, companion cells, phloem parenchyma, and phloem fibers. A series of **sieve-tube cells** (also called sieve-tube elements) are arranged end to end to make up a long sieve tube, which transports organic substances such as sugars and amino acids. The sugars flow from one sieve-tube cell to the next through perforated sieve plates, which are found at

the end junctions between two cells. Although still alive at maturity, the nucleus and other cell components of the sieve-tube cells have disintegrated. **Companion cells** are found alongside the sieve-tube cells, providing them with metabolic support. The companion cells contain more ribosomes and mitochondria than the sieve-tube cells, which lack some cellular organelles.

Ground Tissue

Ground tissue is mostly made up of parenchyma cells, but may also contain collenchyma and sclerenchyma cells that help support the stem. The ground tissue towards the interior of the vascular tissue in a stem or root is known as **pith**, while the layer of tissue between the vascular tissue and the epidermis is known as the **cortex**.

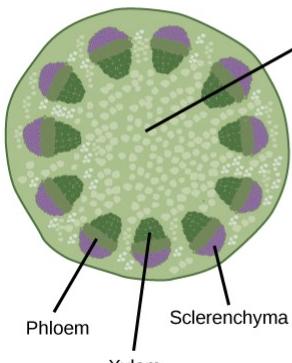
In woody plants, primary growth is followed by secondary growth, which allows the plant stem to increase in thickness or girth. Secondary vascular tissue is added as the plant grows, as well as a cork layer. The bark of a tree extends from the vascular cambium to the epidermis. Lenticels on the bark of this cherry tree enable the woody stem to exchange gases with the surrounding atmosphere. (credit: Roger Griffith) The rate of wood growth increases in summer and decreases in winter, producing a characteristic ring for each year of growth. Seasonal changes in weather patterns can also affect the growth rate—note how the rings vary in thickness.

(credit: Adrian Pingstone)

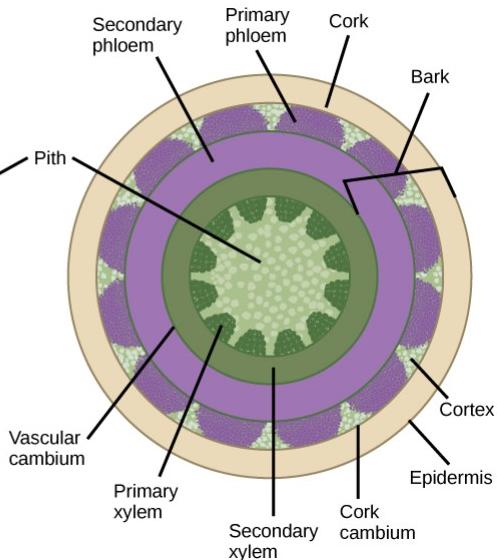
Growth in Stems

Growth in plants occurs as the stems and roots lengthen. Some plants, especially those that are woody, also increase in thickness during their life span. The increase in length of the shoot and the root is referred to as **primary growth**, and is the result of cell division in the shoot apical meristem. **Secondary growth** is characterized by an increase in thickness or girth of the plant, and is caused by cell division in the lateral meristem. [\[link\]](#) shows the areas of primary and secondary growth in a plant. Herbaceous plants mostly undergo primary growth, with hardly any secondary growth or increase in thickness. Secondary growth or “wood” is noticeable in woody plants; it occurs in some dicots, but occurs very rarely in monocots.

Primary growth



Secondary growth



Some plant parts, such as stems and roots, continue to grow throughout a plant's life: a phenomenon called indeterminate growth. Other plant parts, such as leaves and flowers, exhibit determinate growth, which ceases when a plant part reaches a particular size.

Primary Growth

Most primary growth occurs at the apices, or tips, of stems and roots. Primary growth is a result of rapidly dividing cells in the apical meristems at the shoot tip and root tip. Subsequent cell elongation also contributes to primary growth. The growth of shoots and roots during primary growth enables plants to continuously seek water (roots) or sunlight (shoots).

The influence of the apical bud on overall plant growth is known as apical dominance, which diminishes the growth of axillary buds that form along the sides of branches and stems. Most coniferous trees exhibit strong apical dominance, thus producing the typical conical Christmas tree shape. If the apical bud is removed, then the axillary buds will start forming lateral branches. Gardeners make use of this fact when they prune plants by cutting off the tops of branches, thus encouraging the axillary buds to grow out, giving the plant a bushy shape.

Link to Learning



Watch this [BBC Nature video](#) showing how time-lapse photography captures plant growth at high speed.

Secondary Growth

The increase in stem thickness that results from secondary growth is due to the activity of the lateral meristems, which are lacking in herbaceous plants. Lateral meristems include the vascular cambium and, in woody plants, the cork cambium (see [\[link\]](#)). The vascular cambium is located just outside the primary xylem and to the interior of the primary phloem. The cells of the vascular cambium divide and form secondary xylem (tracheids and vessel elements) to the inside, and secondary phloem (sieve elements and companion cells) to the outside. The thickening of the stem that occurs in secondary growth is due to the formation of secondary phloem and secondary xylem by the vascular cambium, plus the action of cork cambium, which forms the tough outermost layer of the stem. The cells of the secondary xylem contain lignin, which provides hardness and strength.

In woody plants, cork cambium is the outermost lateral meristem. It produces cork cells (bark) containing a waxy substance known as suberin that can repel water. The bark protects the plant against physical damage and helps reduce water loss. The cork cambium also produces a layer of cells known as phellogen, which grows inward from the cambium. The cork cambium, cork cells, and phellogen are collectively termed the **periderm**. The periderm substitutes for the epidermis in mature plants. In some plants, the periderm has many openings, known as **lenticels**, which allow

the interior cells to exchange gases with the outside atmosphere ([\[link\]](#)). This supplies oxygen to the living and metabolically active cells of the cortex, xylem and phloem.



Annual Rings

The activity of the vascular cambium gives rise to annual growth rings. During the spring growing season, cells of the secondary xylem have a large internal diameter and their primary cell walls are

not extensively thickened. This is known as early wood, or spring wood. During the fall season, the secondary xylem develops thickened cell walls, forming late wood, or autumn wood, which is denser than early wood. This alternation of early and late wood is due largely to a seasonal decrease in the number of vessel elements and a seasonal increase in the number of tracheids. It results in the formation of an annual ring, which can be seen as a circular ring in the cross section of the stem ([\[link\]](#)). An examination of the number of annual rings and their nature (such as their size and cell wall thickness) can reveal the age of the tree and the prevailing climatic conditions during each season.



Stem modifications enable plants to thrive in a variety of environments. Shown are (a) ginger (*Zingiber officinale*) rhizomes, (b) a carrion flower (*Amorphophallus titanum*) corm (c) Rhodes grass

(*Chloris gayana*) stolons, (d) strawberry (*Fragaria ananassa*) runners, (e) potato (*Solanum tuberosum*) tubers, and (f) red onion (*Allium*) bulbs. (credit a: modification of work by Maja Dumat; credit c: modification of work by Harry Rose; credit d: modification of work by Rebecca Siegel; credit e: modification of work by Scott Bauer, USDA ARS; credit f: modification of work by Stephen Ausmus, USDA ARS) Found in southeastern United States, (a) buckwheat vine (*Brunnichia ovata*) is a weedy plant that climbs with the aid of tendrils. This one is shown climbing up a wooden stake. (b) Thorns are modified branches. (credit a: modification of work by Christopher Meloche, USDA ARS; credit b: modification of work by “macrophile”/Flickr)

Stem Modifications

Some plant species have modified stems that are especially suited to a particular habitat and environment ([\[link\]](#)). A **rhizome** is a modified stem that grows horizontally underground and has nodes and internodes. Vertical shoots may arise from the buds on the rhizome of some plants, such as ginger and ferns. **Corms** are similar to rhizomes, except they are more rounded and fleshy (such as in gladiolus). Corms contain stored food that enables some plants to survive the winter. **Stolons** are stems that run almost parallel to the ground, or just below the surface, and can give rise to new plants at the nodes. **Runners** are a type of stolon that runs above

the ground and produces new clone plants at nodes at varying intervals: strawberries are an example.

Tubers are modified stems that may store starch, as seen in the potato (*Solanum* sp.). Tubers arise as swollen ends of stolons, and contain many adventitious or unusual buds (familiar to us as the “eyes” on potatoes). A **bulb**, which functions as an underground storage unit, is a modification of a stem that has the appearance of enlarged fleshy leaves emerging from the stem or surrounding the base of the stem, as seen in the iris.



Link to Learning



Watch botanist Wendy Hodgson, of Desert Botanical Garden in Phoenix, Arizona, explain how agave plants were cultivated for food hundreds of years ago in the Arizona desert in this [video](#): *Finding the Roots of an Ancient Crop*.

Some aerial modifications of stems are tendrils and thorns ([\[link\]](#)). **Tendrils** are slender, twining strands that enable a plant (like a vine or pumpkin) to seek support by climbing on other surfaces. **Thorns** are modified branches appearing as sharp outgrowths that protect the plant; common examples include roses, Osage orange and devil's walking stick.



(a)



(b)

Section Summary

The stem of a plant bears the leaves, flowers, and

fruits. Stems are characterized by the presence of nodes (the points of attachment for leaves or branches) and internodes (regions between nodes).

Plant organs are made up of simple and complex tissues. The stem has three tissue systems: dermal, vascular, and ground tissue. Dermal tissue is the outer covering of the plant. It contains epidermal cells, stomata, guard cells, and trichomes. Vascular tissue is made up of xylem and phloem tissues and conducts water, minerals, and photosynthetic products. Ground tissue is responsible for photosynthesis and support and is composed of parenchyma, collenchyma, and sclerenchyma cells.

Primary growth occurs at the tips of roots and shoots, causing an increase in length. Woody plants may also exhibit secondary growth, or increase in thickness. In woody plants, especially trees, annual rings may form as growth slows at the end of each season. Some plant species have modified stems that help to store food, propagate new plants, or discourage predators. Rhizomes, corms, stolons, runners, tubers, bulbs, tendrils, and thorns are examples of modified stems.

Art Connections

[\[link\]](#) Which layers of the stem are made of parenchyma cells?

1. cortex and pith
 2. epidermis
 3. sclerenchyma
 4. epidermis and cortex.
-

[\[link\]](#) A and B. The cortex, pith, and epidermis are made of parenchyma cells.

Review Questions

Stem regions at which leaves are attached are called _____.

1. trichomes
 2. lenticels
 3. nodes
 4. internodes
-

C

Which of the following cell types forms most of the inside of a plant?

-
1. meristem cells
 2. collenchyma cells
 3. sclerenchyma cells
 4. parenchyma cells
-

D

Tracheids, vessel elements, sieve-tube cells, and companion cells are components of _____.

1. vascular tissue
 2. meristematic tissue
 3. ground tissue
 4. dermal tissue
-

A

The primary growth of a plant is due to the action of the _____.

1. lateral meristem
 2. vascular cambium
 3. apical meristem
 4. cork cambium
-

C

Which of the following is an example of secondary growth?

1. increase in length
 2. increase in thickness or girth
 3. increase in root hairs
 4. increase in leaf number
-

B

Secondary growth in stems is usually seen in _____.

1. monocots
 2. dicots
 3. both monocots and dicots
 4. neither monocots nor dicots
-

B

Free Response

Describe the roles played by stomata and guard cells. What would happen to a plant if these cells did not function correctly?

Stomata allow gases to enter and exit the plant. Guard cells regulate the opening and closing of stomata. If these cells did not function correctly, a plant could not get the carbon dioxide needed for photosynthesis, nor could it release the oxygen produced by photosynthesis.

Compare the structure and function of xylem to that of phloem.

Xylem is made up tracheids and vessel elements, which are cells that transport water and dissolved minerals and that are dead at maturity. Phloem is made up of sieve-tube cells and companion cells, which transport carbohydrates and are alive at maturity.

Explain the role of the cork cambium in woody plants.

In woody plants, the cork cambium is the outermost lateral meristem; it produces new cells towards the interior, which enables the plant to increase in girth. The cork cambium also produces cork cells towards the exterior, which protect the plant from physical damage while reducing water loss.

What is the function of lenticels?

In woody stems, lenticels allow internal cells to exchange gases with the outside atmosphere.

Besides the age of a tree, what additional information can annual rings reveal?

Annual rings can also indicate the climate conditions that prevailed during each growing season.

Give two examples of modified stems and explain how each example benefits the plant.

Answers will vary. Rhizomes, stolons, and runners can give rise to new plants. Corms, tubers, and bulbs can also produce new plants and can store food. Tendrils help a plant to climb, while thorns discourage herbivores.

Glossary

apical bud
bud formed at the tip of the shoot

axillary bud

bud located in the axil: the stem area where the petiole connects to the stem

bark

tough, waterproof, outer epidermal layer of cork cells

bulb

modified underground stem that consists of a large bud surrounded by numerous leaf scales

collenchyma cell

elongated plant cell with unevenly thickened walls; provides structural support to the stem and leaves

companion cell

phloem cell that is connected to sieve-tube cells; has large amounts of ribosomes and mitochondrion

corm

rounded, fleshy underground stem that contains stored food

cortex

ground tissue found between the vascular tissue and the epidermis in a stem or root

epidermis

single layer of cells found in plant dermal

tissue; covers and protects underlying tissue

guard cells

paired cells on either side of a stoma that control stomatal opening and thereby regulate the movement of gases and water vapor

internode

region between nodes on the stem

lenticel

opening on the surface of mature woody stems that facilitates gas exchange

node

point along the stem at which leaves, flowers, or aerial roots originate

parenchyma cell

most common type of plant cell; found in the stem, root, leaf, and in fruit pulp; site of photosynthesis and starch storage

periderm

outermost covering of woody stems; consists of the cork cambium, cork cells, and the phellogen

pith

ground tissue found towards the interior of the vascular tissue in a stem or root

primary growth

growth resulting in an increase in length of the stem and the root; caused by cell division in the shoot or root apical meristem

rhizome

modified underground stem that grows horizontally to the soil surface and has nodes and internodes

runner

stolon that runs above the ground and produces new clone plants at nodes

sclerenchyma cell

plant cell that has thick secondary walls and provides structural support; usually dead at maturity

secondary growth

growth resulting in an increase in thickness or girth; caused by the lateral meristem and cork cambium

sieve-tube cell

phloem cell arranged end to end to form a sieve tube that transports organic substances such as sugars and amino acids

stolon

modified stem that runs parallel to the ground and can give rise to new plants at the nodes

tendril

modified stem consisting of slender, twining strands used for support or climbing

thorn

modified stem branch appearing as a sharp outgrowth that protects the plant

tracheid

xylem cell with thick secondary walls that helps transport water

trichome

hair-like structure on the epidermal surface

tuber

modified underground stem adapted for starch storage; has many adventitious buds

vessel element

xylem cell that is shorter than a tracheid and has thinner walls

Roots

By the end of this section, you will be able to do the following:

- Identify the two types of root systems
- Describe the three zones of the root tip and summarize the role of each zone in root growth
- Describe the structure of the root
- List and describe examples of modified roots

The roots of seed plants have three major functions: anchoring the plant to the soil, absorbing water and minerals and transporting them upwards, and storing the products of photosynthesis. Some roots are modified to absorb moisture and exchange gases. Most roots are underground. Some plants, however, also have **adventitious roots**, which emerge above the ground from the shoot.

(a) Tap root systems have a main root that grows down, while (b) fibrous root systems consist of many small roots. (credit b: modification of work by “Austen Squarepants”/Flickr)

Types of Root Systems

Root systems are mainly of two types ([\[link\]](#)).

Dicots have a tap root system, while monocots have a fibrous root system. A **tap root system** has a main root that grows down vertically, and from which many smaller lateral roots arise. Dandelions are a

good example; their tap roots usually break off when trying to pull these weeds, and they can regrow another shoot from the remaining root. A tap root system penetrates deep into the soil. In contrast, a **fibrous root system** is located closer to the soil surface, and forms a dense network of roots that also helps prevent soil erosion (lawn grasses are a good example, as are wheat, rice, and corn). Some plants have a combination of tap roots and fibrous roots. Plants that grow in dry areas often have deep root systems, whereas plants growing in areas with abundant water are likely to have shallower root systems.

(a) Taproot system



(b) Fibrous root system



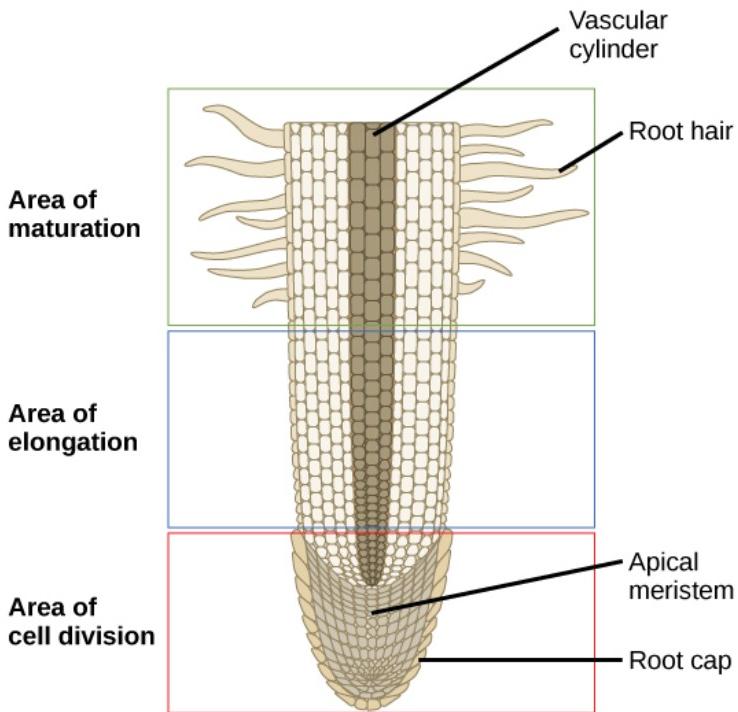
A longitudinal view of the root reveals the zones of cell division, elongation, and maturation. Cell division occurs in the apical meristem. Staining reveals different cell types in this light micrograph

of a wheat (*Triticum*) root cross section. Sclerenchyma cells of the exodermis and xylem cells stain red, and phloem cells stain blue. Other cell types stain black. The stele, or vascular tissue, is the area inside endodermis (indicated by a green ring). Root hairs are visible outside the epidermis. (credit: scale-bar data from Matt Russell) In (left) typical dicots, the vascular tissue forms an X shape in the center of the root. In (right) typical monocots, the phloem cells and the larger xylem cells form a characteristic ring around the central pith.

Root Growth and Anatomy

Root growth begins with seed germination. When the plant embryo emerges from the seed, the radicle of the embryo forms the root system. The tip of the root is protected by the **root cap**, a structure exclusive to roots and unlike any other plant structure. The root cap is continuously replaced because it gets damaged easily as the root pushes through soil. The root tip can be divided into three zones: a zone of cell division, a zone of elongation, and a zone of maturation and differentiation ([\[link\]](#)). The zone of cell division is closest to the root tip; it is made up of the actively dividing cells of the root meristem. The zone of elongation is where the newly formed cells increase in length, thereby lengthening the root. Beginning at the first root hair is the zone of cell maturation where the root cells begin to differentiate into special cell

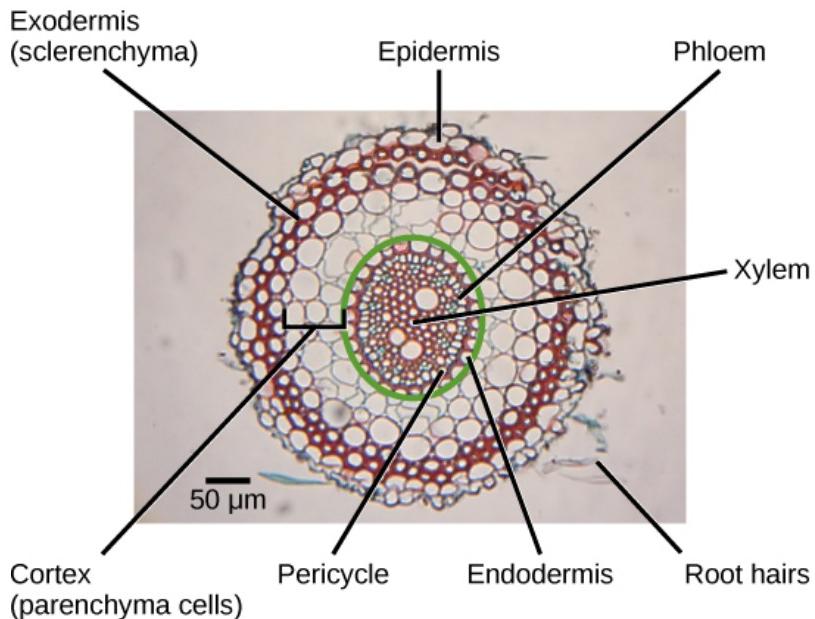
types. All three zones are in the first centimeter or so of the root tip.



The root has an outer layer of cells called the epidermis, which surrounds areas of ground tissue and vascular tissue. The epidermis provides protection and helps in absorption. **Root hairs**, which are extensions of root epidermal cells, increase the surface area of the root, greatly contributing to the absorption of water and minerals.

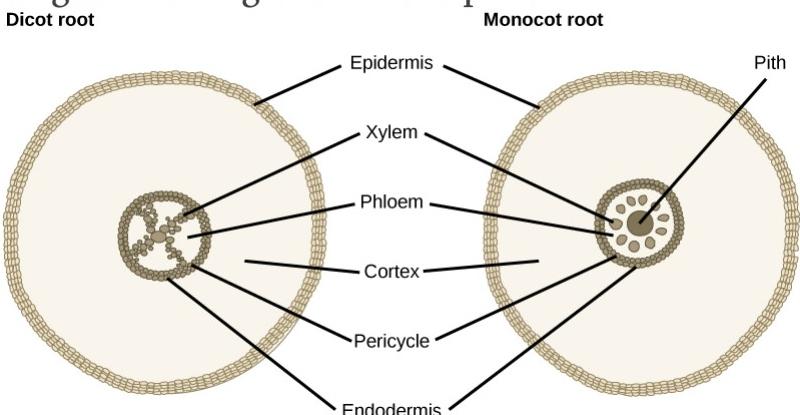
Inside the root, the ground tissue forms two regions: the cortex and the pith ([\[link\]](#)). Compared to stems, roots have lots of cortex and little pith. Both regions

include cells that store photosynthetic products. The cortex is between the epidermis and the vascular tissue, whereas the pith lies between the vascular tissue and the center of the root.



The vascular tissue in the root is arranged in the inner portion of the root, which is called the **stele** ([\[link\]](#)). A layer of cells known as the **endodermis** separates the stele from the ground tissue in the outer portion of the root. The endodermis is exclusive to roots, and serves as a checkpoint for materials entering the root's vascular system. A waxy substance called suberin is present on the walls of the endodermal cells. This waxy region, known as the **Casparian strip**, forces water and solutes to cross the plasma membranes of endodermal cells instead of slipping between the

cells. This ensures that only materials required by the root pass through the endodermis, while toxic substances and pathogens are generally excluded. The outermost cell layer of the root's vascular tissue is the **pericycle**, an area that can give rise to lateral roots. In dicot roots, the xylem and phloem of the stele are arranged alternately in an X shape, whereas in monocot roots, the vascular tissue is arranged in a ring around the pith.



Many vegetables are modified roots. The (a) banyan tree, also known as the strangler fig, begins life as an epiphyte in a host tree. Aerial roots extend to the ground and support the growing plant, which eventually strangles the host tree. The (b) screwpine develops aboveground roots that help support the plant in sandy soils. (credit a: modification of work by "psyberartist"/Flickr; credit b: modification of work by David Eikhoff)

Root Modifications

Root structures may be modified for specific

purposes. For example, some roots are bulbous and store starch. Aerial roots and prop roots are two forms of aboveground roots that provide additional support to anchor the plant. Tap roots, such as carrots, turnips, and beets, are examples of roots that are modified for food storage ([\[link\]](#)).



Epiphytic roots enable a plant to grow on another plant. For example, the epiphytic roots of orchids develop a spongy tissue to absorb moisture. The banyan tree (*Ficus* sp.) begins as an epiphyte, germinating in the branches of a host tree; aerial roots develop from the branches and eventually reach the ground, providing additional support ([\[link\]](#)). In screwpine (*Pandanus* sp.), a palm-like tree that grows in sandy tropical soils, aboveground prop roots develop from the nodes to provide additional support.



(a)



(b)

Section Summary

Roots help to anchor a plant, absorb water and minerals, and serve as storage sites for food.

Taproots and fibrous roots are the two main types of root systems. In a taproot system, a main root grows vertically downward with a few lateral roots.

Fibrous root systems arise at the base of the stem, where a cluster of roots forms a dense network that is shallower than a taproot. The growing root tip is protected by a root cap. The root tip has three main zones: a zone of cell division (cells are actively dividing), a zone of elongation (cells increase in length), and a zone of maturation (cells differentiate to form different kinds of cells). Root vascular tissue conducts water, minerals, and sugars. In some habitats, the roots of certain plants may be modified to form aerial roots or epiphytic roots.

Review Questions

Roots that enable a plant to grow on another plant are called ____.

1. epiphytic roots
 2. prop roots
 3. adventitious roots
 4. aerial roots
-

A

The _____ forces selective uptake of minerals in the root.

1. pericycle
 2. epidermis
 3. endodermis
 4. root cap
-

C

Newly-formed root cells begin to form different cell types in the _____.

1. zone of elongation
2. zone of maturation
3. root meristem
4. zone of cell division

B

Critical Thinking Questions

Compare a tap root system with a fibrous root system. For each type, name a plant that provides a food in the human diet. Which type of root system is found in monocots? Which type of root system is found in dicots?

A tap root system has a single main root that grows down. A fibrous root system forms a dense network of roots that is closer to the soil surface. An example of a tap root system is a carrot. Grasses such as wheat, rice, and corn are examples of fibrous root systems. Fibrous root systems are found in monocots; tap root systems are found in dicots.

What might happen to a root if the pericycle disappeared?

The root would not be able to produce lateral roots.

Glossary

adventitious root

aboveground root that arises from a plant part other than the radicle of the plant embryo

Casparian strip

waxy coating that forces water to cross endodermal plasma membranes before entering the vascular cylinder, instead of moving between endodermal cells

endodermis

layer of cells in the root that forms a selective barrier between the ground tissue and the vascular tissue, allowing water and minerals to enter the root while excluding toxins and pathogens

fibrous root system

type of root system in which the roots arise from the base of the stem in a cluster, forming a dense network of roots; found in monocots

pericycle

outer boundary of the stele from which lateral roots can arise

root cap

protective cells covering the tip of the

growing root

root hair

hair-like structure that is an extension of epidermal cells; increases the root surface area and aids in absorption of water and minerals

stele

inner portion of the root containing the vascular tissue; surrounded by the endodermis

tap root system

type of root system with a main root that grows vertically with few lateral roots; found in dicots

Leaves

By the end of this section, you will be able to do the following:

- Identify the parts of a typical leaf
- Describe the internal structure and function of a leaf
- Compare and contrast simple leaves and compound leaves
- List and describe examples of modified leaves

Leaves are the main sites for photosynthesis: the process by which plants synthesize food. Most leaves are usually green, due to the presence of chlorophyll in the leaf cells. However, some leaves may have different colors, caused by other plant pigments that mask the green chlorophyll.

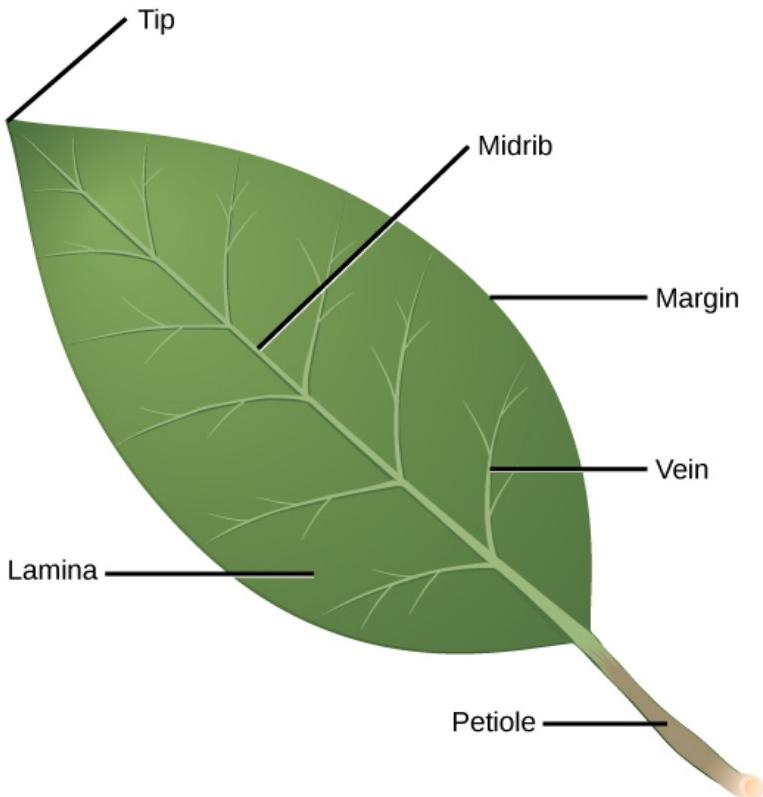
The thickness, shape, and size of leaves are adapted to the environment. Each variation helps a plant species maximize its chances of survival in a particular habitat. Usually, the leaves of plants growing in tropical rainforests have larger surface areas than those of plants growing in deserts or very cold conditions, which are likely to have a smaller surface area to minimize water loss.

Deceptively simple in appearance, a leaf is a highly efficient structure. (a) Tulip (*Tulipa*), a monocot, has leaves with parallel venation. The netlike venation in this (b) linden (*Tilia cordata*) leaf distinguishes it as a dicot. The (c) *Ginkgo biloba* tree has

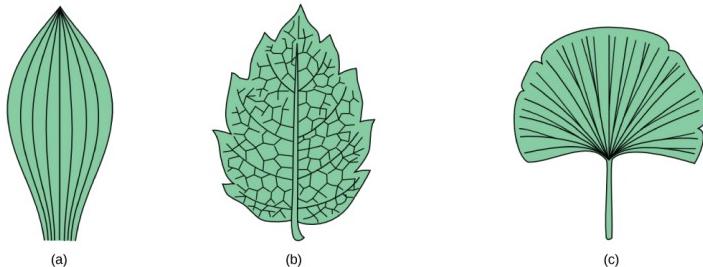
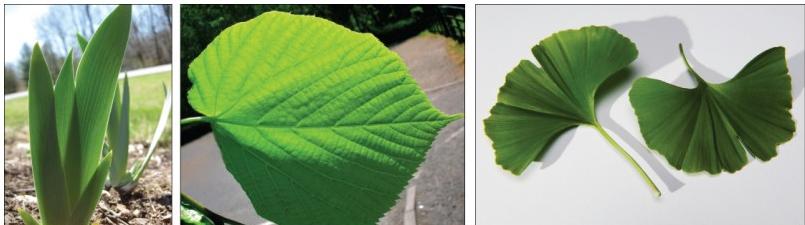
dichotomous venation. (credit a photo: modification of work by “Drewboy64”/Wikimedia Commons; credit b photo: modification of work by Roger Griffith; credit c photo: modification of work by "geishaboy500"/Flickr; credit abc illustrations: modification of work by Agnieszka Kwiecień)

Structure of a Typical Leaf

Each leaf typically has a leaf blade called the **lamina**, which is also the widest part of the leaf. Some leaves are attached to the plant stem by a **petiole**. Leaves that do not have a petiole and are directly attached to the plant stem are called **sessile** leaves. Small green appendages usually found at the base of the petiole are known as **stipules**. Most leaves have a midrib, which travels the length of the leaf and branches to each side to produce veins of vascular tissue. The edge of the leaf is called the margin. [\[link\]](#) shows the structure of a typical eudicot leaf.



Within each leaf, the vascular tissue forms veins. The arrangement of veins in a leaf is called the **venation** pattern. Monocots and dicots differ in their patterns of venation ([\[link\]](#)). Monocots have parallel venation; the veins run in straight lines across the length of the leaf without converging at a point. In dicots, however, the veins of the leaf have a net-like appearance, forming a pattern known as reticulate venation. One extant plant, the *Ginkgo biloba*, has dichotomous venation where the veins fork.



Leaf Arrangement

The arrangement of leaves on a stem is known as **phyllotaxy**. The number and placement of a plant's leaves will vary depending on the species, with each species exhibiting a characteristic leaf arrangement. Leaves are classified as either alternate, spiral, or opposite. Plants that have only one leaf per node have leaves that are said to be either alternate—meaning the leaves alternate on each side of the stem in a flat plane—or spiral, meaning the leaves are arrayed in a spiral along the stem. In an opposite leaf arrangement, two leaves arise at the same point, with the leaves connecting opposite each other along the branch. If there are three or more leaves connected at a node, the leaf arrangement is classified as **whorled**.

Leaves may be simple or compound. In simple

leaves, the lamina is continuous. The (a) banana plant (*Musa* sp.) has simple leaves. In compound leaves, the lamina is separated into leaflets.

Compound leaves may be palmate or pinnate. In (b) palmately compound leaves, such as those of the horse chestnut (*Aesculus hippocastanum*), the leaflets branch from the petiole. In (c) pinnately compound leaves, the leaflets branch from the midrib, as on a scrub hickory (*Carya floridana*). The (d) honey locust has double compound leaves, in which leaflets branch from the veins. (credit a: modification of work by "BazzaDaRambler"/Flickr; credit b: modification of work by Roberto Verzo; credit c: modification of work by Eric Dion; credit d: modification of work by Valerie Lykes)

Leaf Form

Leaves may be simple or compound ([\[link\]](#)). In a **simple leaf**, the blade is either completely undivided—as in the banana leaf—or it has lobes, but the separation does not reach the midrib, as in the maple leaf. In a **compound leaf**, the leaf blade is completely divided, forming leaflets, as in the locust tree. Each leaflet may have its own stalk, but is attached to the rachis. A **palmately compound leaf** resembles the palm of a hand, with leaflets radiating outwards from one point. Examples include the leaves of poison ivy, the buckeye tree, or the familiar houseplant *Schefflera* sp. (common name “umbrella plant”). **Pinnately compound**

leaves take their name from their feather-like appearance; the leaflets are arranged along the midrib, as in rose leaves (*Rosa* sp.), or the leaves of hickory, pecan, ash, or walnut trees.



(a) Simple



(b) Palmately compound



(c) Pinnately compound



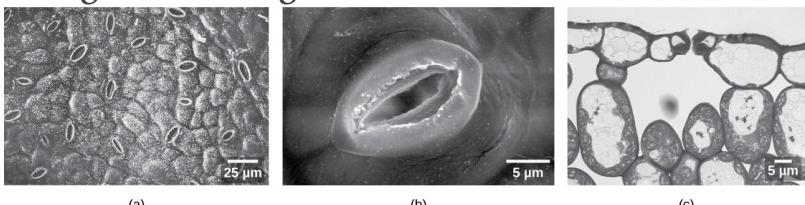
(d) Doubly compound

Visualized at 500x with a scanning electron microscope, several stomata are clearly visible on (a) the surface of this sumac (*Rhus glabra*) leaf. At 5,000x magnification, the guard cells of (b) a single stoma from lyre-leaved sand cress (*Arabidopsis lyrata*) have the appearance of lips that surround the opening. In this (c) light micrograph cross-section of an *A. lyrata* leaf, the guard cell pair is visible along with the large, sub-stomatal air space in the leaf. (credit: modification of work by Robert R. Wise;

part c scale-bar data from Matt Russell) Trichomes give leaves a fuzzy appearance as in this (a) sundew (*Drosera* sp.). Leaf trichomes include (b) branched trichomes on the leaf of *Arabidopsis lyrata* and (c) multibranched trichomes on a mature *Quercus marilandica* leaf. (credit a: John Freeland; credit b, c: modification of work by Robert R. Wise; scale-bar data from Matt Russell) In the (a) leaf drawing, the central mesophyll is sandwiched between an upper and lower epidermis. The mesophyll has two layers: an upper palisade layer comprised of tightly packed, columnar cells, and a lower spongy layer, comprised of loosely packed, irregularly shaped cells. Stomata on the leaf underside allow gas exchange. A waxy cuticle covers all aerial surfaces of land plants to minimize water loss. These leaf layers are clearly visible in the (b) scanning electron micrograph. The numerous small bumps in the palisade parenchyma cells are chloroplasts. Chloroplasts are also present in the spongy parenchyma, but are not as obvious. The bumps protruding from the lower surface of the leave are glandular trichomes, which differ in structure from the stalked trichomes in [\[link\]](#). (credit b: modification of work by Robert R. Wise) This scanning electron micrograph shows xylem and phloem in the leaf vascular bundle from the lyre-leaved sand cress (*Arabidopsis lyrata*). (credit: modification of work by Robert R. Wise; scale-bar data from Matt Russell)

Leaf Structure and Function

The outermost layer of the leaf is the epidermis; it is present on both sides of the leaf and is called the upper and lower epidermis, respectively. Botanists call the upper side the adaxial surface (or adaxis) and the lower side the abaxial surface (or abaxis). The epidermis helps in the regulation of gas exchange. It contains stomata ([\[link\]](#)): openings through which the exchange of gases takes place. Two guard cells surround each stoma, regulating its opening and closing.



(a)

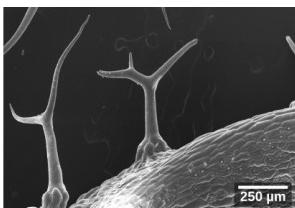
(b)

(c)

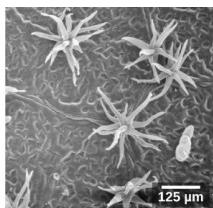
The epidermis is usually one cell layer thick; however, in plants that grow in very hot or very cold conditions, the epidermis may be several layers thick to protect against excessive water loss from transpiration. A waxy layer known as the **cuticle** covers the leaves of all plant species. The cuticle reduces the rate of water loss from the leaf surface. Other leaves may have small hairs (trichomes) on the leaf surface. Trichomes help to deter herbivory by restricting insect movements, or by storing toxic or bad-tasting compounds; they can also reduce the rate of transpiration by blocking air flow across the leaf surface ([\[link\]](#)).



(a)

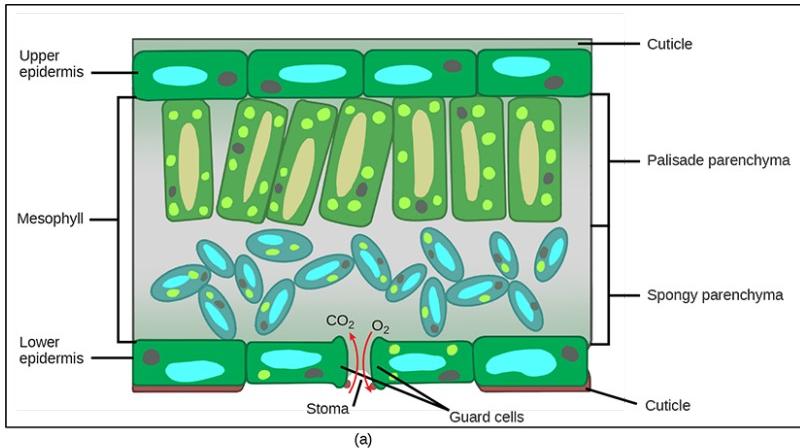


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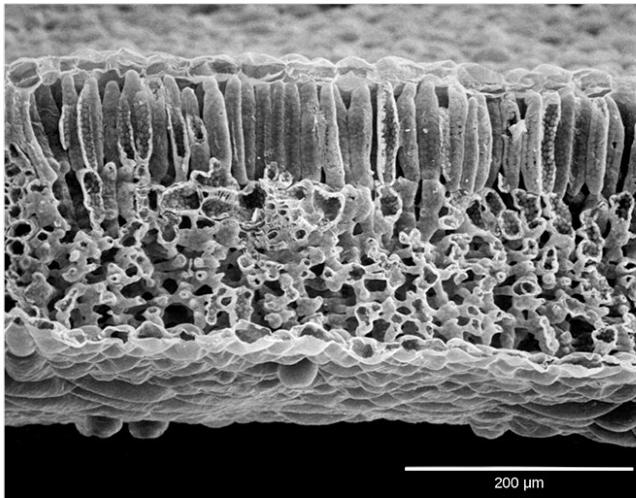


(c)

Below the epidermis of dicot leaves are layers of cells known as the mesophyll, or “middle leaf.” The mesophyll of most leaves typically contains two arrangements of parenchyma cells: the palisade parenchyma and spongy parenchyma ([\[link\]](#)). The palisade parenchyma (also called the palisade mesophyll) has column-shaped, tightly packed cells, and may be present in one, two, or three layers. Below the palisade parenchyma are loosely arranged cells of an irregular shape. These are the cells of the spongy parenchyma (or spongy mesophyll). The air space found between the spongy parenchyma cells allows gaseous exchange between the leaf and the outside atmosphere through the stomata. In aquatic plants, the intercellular spaces in the spongy parenchyma help the leaf float. Both layers of the mesophyll contain many chloroplasts. Guard cells are the only epidermal cells to contain chloroplasts.

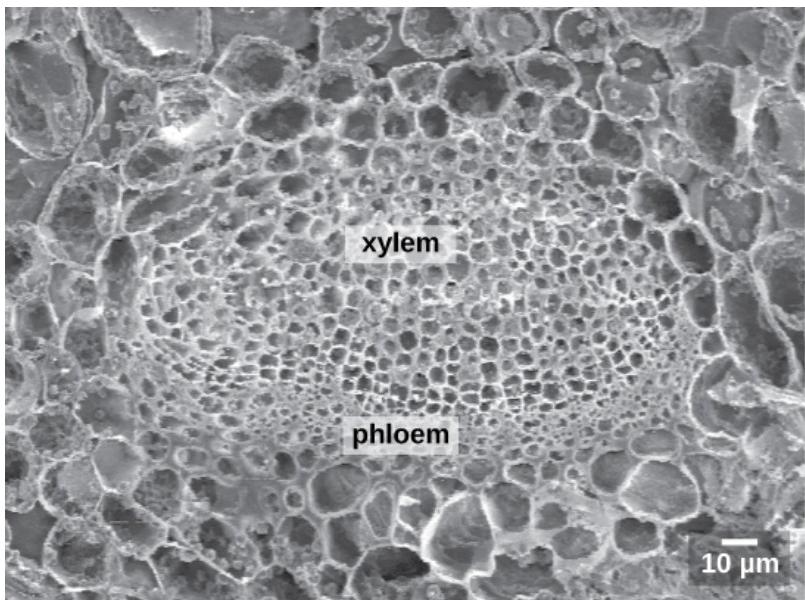


(a)



(b)

Like the stem, the leaf contains vascular bundles composed of xylem and phloem ([\[link\]](#)). The xylem consists of tracheids and vessels, which transport water and minerals to the leaves. The phloem transports the photosynthetic products from the leaf to the other parts of the plant. A single vascular bundle, no matter how large or small, always contains both xylem and phloem tissues.



Leaf Adaptations

Coniferous plant species that thrive in cold environments, like spruce, fir, and pine, have leaves that are reduced in size and needle-like in appearance. These needle-like leaves have sunken stomata and a smaller surface area: two attributes that aid in reducing water loss. In hot climates, plants such as cacti have leaves that are reduced to spines, which in combination with their succulent stems, help to conserve water. Many aquatic plants have leaves with wide lamina that can float on the surface of the water, and a thick waxy cuticle on the leaf surface that repels water.

Link to Learning

Watch “The Pale Pitcher Plant” episode of the [video](#) series *Plants Are Cool, Too*, a Botanical Society of America video about a carnivorous plant species found in Louisiana.

Evolution Connection

Plant Adaptations in Resource-Deficient Environments

Roots, stems, and leaves are structured to ensure that a plant can obtain the required sunlight, water, soil nutrients, and oxygen resources. Some remarkable adaptations have evolved to enable plant species to thrive in less than ideal habitats, where one or more of these resources is in short supply.

In tropical rainforests, light is often scarce, since many trees and plants grow close together and block much of the sunlight from reaching the forest floor. Many tropical plant species have exceptionally broad leaves to maximize the capture of sunlight. Other species are epiphytes: plants that grow on other plants that serve as a physical support. Such plants are able to grow high up in the canopy atop the branches of other trees, where sunlight is more plentiful. Epiphytes live on rain and minerals collected in the branches and leaves of the supporting plant. Bromeliads (members of the pineapple family), ferns, and orchids are

examples of tropical epiphytes ([\[link\]](#)). Many epiphytes have specialized tissues that enable them to efficiently capture and store water.

One of the most well known bromeliads is Spanish moss (*Tillandsia usneoides*), seen here in an oak tree. (credit: Kristine Paulus)



Some plants have special adaptations that help them to survive in nutrient-poor environments. Carnivorous plants, such as the Venus flytrap and the pitcher plant ([\[link\]](#)), grow in bogs where the soil is low in nitrogen. In these plants, leaves are

modified to capture insects. The insect-capturing leaves may have evolved to provide these plants with a supplementary source of much-needed nitrogen.

The (a) Venus flytrap has modified leaves that can capture insects. When an unlucky insect touches the trigger hairs inside the leaf, the trap suddenly closes. The opening of the (b) pitcher plant is lined with a slippery wax. Insects crawling on the lip slip and fall into a pool of water in the bottom of the pitcher, where they are digested by bacteria. The plant then absorbs the smaller molecules. (credit a: modification of work by Peter Shanks; credit b: modification of work by Tim Mansfield)



(a)



(b)

Many swamp plants have adaptations that enable them to thrive in wet areas, where their roots grow submerged underwater. In these aquatic areas, the soil is unstable and little oxygen is available to reach the roots. Trees such as mangroves (*Rhizophora* sp.) growing in coastal waters produce aboveground roots that help support the tree ([\[link\]](#)). Some species of mangroves, as well as cypress trees, have pneumatophores: upward-

growing roots containing pores and pockets of tissue specialized for gas exchange. Wild rice is an aquatic plant with large air spaces in the root cortex. The air-filled tissue—called aerenchyma—provides a path for oxygen to diffuse down to the root tips, which are embedded in oxygen-poor bottom sediments.

The branches of (a) mangrove trees develop aerial roots, which descend to the ground and help to anchor the trees. (b) Cypress trees and some mangrove species have upward-growing roots called pneumatophores that are involved in gas exchange. Aquatic plants such as (c) wild rice have large spaces in the root cortex called aerenchyma, visualized here using scanning electron microscopy. (credit a: modification of work by Roberto Verzo; credit b: modification of work by Duane Burdick; credit c: modification of work by Robert R. Wise)



(a)



(b)



(c)

Link to Learning

Watch *Venus Flytraps: Jaws of Death*, an extraordinary BBC close-up of the Venus flytrap in action.

Section Summary

Leaves are the main site of photosynthesis. A typical leaf consists of a lamina (the broad part of the leaf, also called the blade) and a petiole (the stalk that attaches the leaf to a stem). The arrangement of leaves on a stem, known as phyllotaxy, enables maximum exposure to sunlight. Each plant species has a characteristic leaf arrangement and form. The pattern of leaf arrangement may be alternate, opposite, or spiral, while leaf form may be simple or compound. Leaf tissue consists of the epidermis, which forms the outermost cell layer, and mesophyll and vascular tissue, which make up the inner portion of the leaf. In some plant species, leaf form is modified to form structures such as tendrils, spines, bud scales, and needles.

Review Questions

The stalk of a leaf is known as the _____.

-
- 1. petiole
 - 2. lamina
 - 3. stipule
 - 4. rachis
-

A

Leaflets are a characteristic of _____ leaves.

- 1. alternate
 - 2. whorled
 - 3. compound
 - 4. opposite
-

C

Cells of the _____ contain chloroplasts.

- 1. epidermis
 - 2. vascular tissue
 - 3. stomata
 - 4. mesophyll
-

D

Which of the following is most likely to be

found in a desert environment?

1. broad leaves to capture sunlight
 2. spines instead of leaves
 3. needle-like leaves
 4. wide, flat leaves that can float
-

B

Critical Thinking Questions

How do dicots differ from monocots in terms of leaf structure?

Monocots have leaves with parallel venation, and dicots have leaves with reticulate, net-like venation.

Describe an example of a plant with leaves that are adapted to cold temperatures.

Conifers such as spruce, fir, and pine have needle-shaped leaves with sunken stomata, helping to reduce water loss.

Glossary

compound leaf

leaf in which the leaf blade is subdivided to form leaflets, all attached to the midrib

cuticle

waxy protective layer on the leaf surface

lamina

leaf blade

palmately compound leaf

leaf type with leaflets that emerge from a point, resembling the palm of a hand

petiole

stalk of the leaf

phyllotaxy

arrangement of leaves on a stem

pinnately compound leaf

leaf type with a divided leaf blade consisting of leaflets arranged on both sides of the midrib

sessile

leaf without a petiole that is attached directly to the plant stem

simple leaf

leaf type in which the lamina is completely undivided or merely lobed

stipule

small green structure found on either side of the leaf stalk or petiole

venation

pattern of veins in a leaf; may be parallel (as in monocots), reticulate (as in dicots), or dichotomous (as in *Ginkgo biloba*)

whorled

pattern of leaf arrangement in which three or more leaves are connected at a node

The Soil and Plant Nutrition

By the end of this section, you will be able to:

- Describe how soils are formed
- Explain soil composition
- Describe a soil profile

Plants obtain inorganic elements from the soil, which serves as a natural medium for land plants. **Soil** is the outer loose layer that covers the surface of Earth. Soil quality is a major determinant, along with climate, of plant distribution and growth. Soil quality depends not only on the chemical composition of the soil, but also the topography (regional surface features) and the presence of living organisms. In agriculture, the history of the soil, such as the cultivating practices and previous crops, modify the characteristics and fertility of that soil.

Soil develops very slowly over long periods of time, and its formation results from natural and environmental forces acting on mineral, rock, and organic compounds. Soils can be divided into two groups: **organic soils** are those that are formed from sedimentation and primarily composed of organic matter, while those that are formed from the weathering of rocks and are primarily composed of inorganic material are called **mineral soils**. Mineral soils are predominant in terrestrial ecosystems, where soils may be covered by water for part of the year or exposed to the atmosphere.

Soil Composition

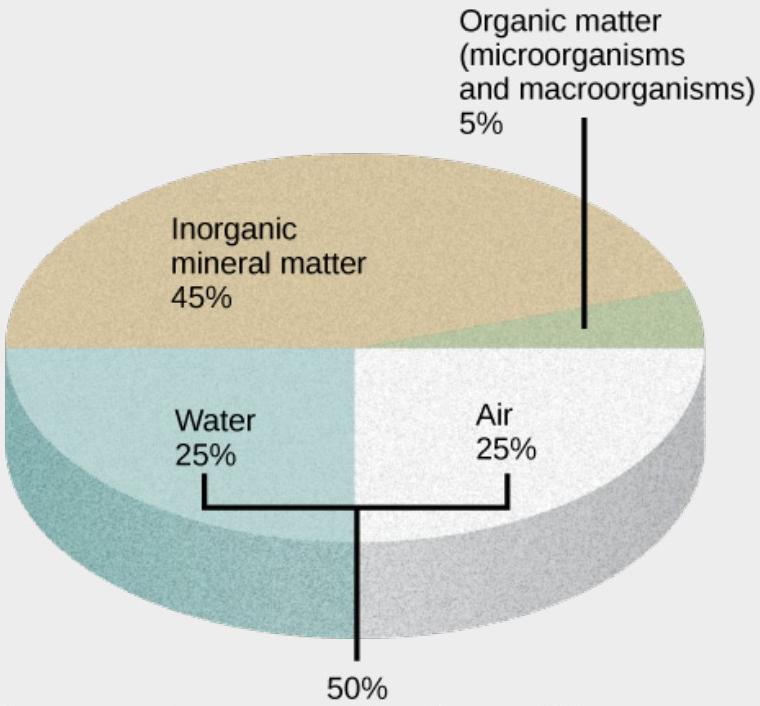
Soil consists of these major components ([\[link\]](#)):

- inorganic mineral matter, about 40 to 45 percent of the soil volume
- organic matter, about 5 percent of the soil volume
- water and air, about 50 percent of the soil volume

The amount of each of the four major components of soil depends on the amount of vegetation, soil compaction, and water present in the soil. A good healthy soil has sufficient air, water, minerals, and organic material to promote and sustain plant life.

Art Connection

The four major components of soil are shown: inorganic minerals, organic matter, water, and air.



Soil compaction can result when soil is compressed by heavy machinery or even foot traffic. How might this compaction change the soil composition?

The organic material of soil, called **humus**, is made up of microorganisms (dead and alive), and dead animals and plants in varying stages of decay. Humus improves soil structure and provides plants with water and minerals. The inorganic material of soil consists of rock, slowly broken down into smaller particles that vary in size. Soil particles that are 0.1 to 2 mm in diameter are **sand**. Soil particles between 0.002 and 0.1 mm are called **silt**, and even

smaller particles, less than 0.002 mm in diameter, are called **clay**. Some soils have no dominant particle size and contain a mixture of sand, silt, and humus; these soils are called **loams**.

Link to Learning



Explore this [interactive map](#) from the USDA's National Cooperative Soil Survey to access soil data for almost any region in the United States.

Soil Formation

Soil formation is the consequence of a combination of biological, physical, and chemical processes. Soil should ideally contain 50 percent solid material and 50 percent pore space. About one-half of the pore space should contain water, and the other half

should contain air. The organic component of soil serves as a cementing agent, returns nutrients to the plant, allows soil to store moisture, makes soil tillable for farming, and provides energy for soil microorganisms. Most soil microorganisms—bacteria, algae, or fungi—are dormant in dry soil, but become active once moisture is available.

Soil distribution is not homogenous because its formation results in the production of layers; together, the vertical section of a soil is called the **soil profile**. Within the soil profile, soil scientists define zones called horizons. A **horizon** is a soil layer with distinct physical and chemical properties that differ from those of other layers. Five factors account for soil formation: parent material, climate, topography, biological factors, and time.

Parent Material

The organic and inorganic material in which soils form is the **parent material**. Mineral soils form directly from the weathering of **bedrock**, the solid rock that lies beneath the soil, and therefore, they have a similar composition to the original rock. Other soils form in materials that came from elsewhere, such as sand and glacial drift. Materials located in the depth of the soil are relatively unchanged compared with the deposited material. Sediments in rivers may have different characteristics, depending on whether the stream

moves quickly or slowly. A fast-moving river could have sediments of rocks and sand, whereas a slow-moving river could have fine-textured material, such as clay.

Climate

Temperature, moisture, and wind cause different patterns of weathering and therefore affect soil characteristics. The presence of moisture and nutrients from weathering will also promote biological activity: a key component of a quality soil.

Topography

Regional surface features (familiarly called “the lay of the land”) can have a major influence on the characteristics and fertility of a soil. Topography affects water runoff, which strips away parent material and affects plant growth. Steep soils are more prone to erosion and may be thinner than soils that are relatively flat or level.

Biological factors

The presence of living organisms greatly affects soil formation and structure. Animals and microorganisms can produce pores and crevices, and plant roots can penetrate into crevices to produce

more fragmentation. Plant secretions promote the development of microorganisms around the root, in an area known as the **rhizosphere**. Additionally, leaves and other material that fall from plants decompose and contribute to soil composition.

Time

Time is an important factor in soil formation because soils develop over long periods. Soil formation is a dynamic process. Materials are deposited over time, decompose, and transform into other materials that can be used by living organisms or deposited onto the surface of the soil.

The San Joaquin soil profile has an O horizon, A horizon, B horizon, and C horizon. (credit: modification of work by USDA)

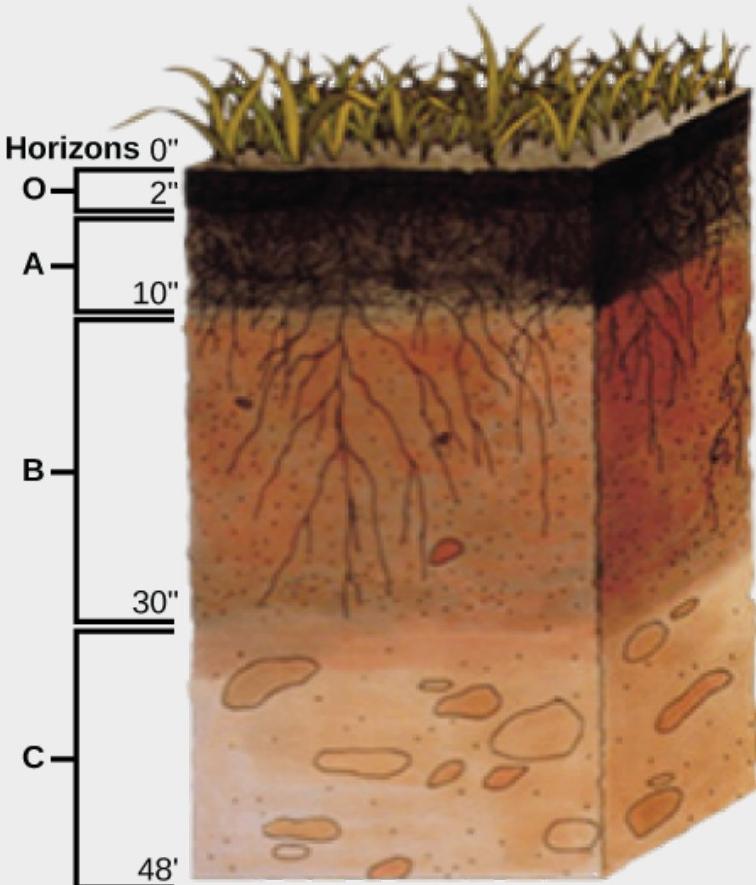
Physical Properties of the Soil

Soils are named and classified based on their horizons. The soil profile has four distinct layers: 1) O horizon; 2) A horizon; 3) B horizon, or subsoil; and 4) C horizon, or soil base ([\[link\]](#)). The **O horizon** has freshly decomposing organic matter—humus—at its surface, with decomposed vegetation at its base. Humus enriches the soil with nutrients and enhances soil moisture retention. Topsoil—the top layer of soil—is usually two to three inches deep, but this depth can vary considerably. For

instance, river deltas like the Mississippi River delta have deep layers of topsoil. Topsoil is rich in organic material; microbial processes occur there, and it is the “workhorse” of plant production. The **A horizon** consists of a mixture of organic material with inorganic products of weathering, and it is therefore the beginning of true mineral soil. This horizon is typically darkly colored because of the presence of organic matter. In this area, rainwater percolates through the soil and carries materials from the surface. The **B horizon** is an accumulation of mostly fine material that has moved downward, resulting in a dense layer in the soil. In some soils, the B horizon contains nodules or a layer of calcium carbonate. The **C horizon**, or soil base, includes the parent material, plus the organic and inorganic material that is broken down to form soil. The parent material may be either created in its natural place, or transported from elsewhere to its present location. Beneath the C horizon lies bedrock.

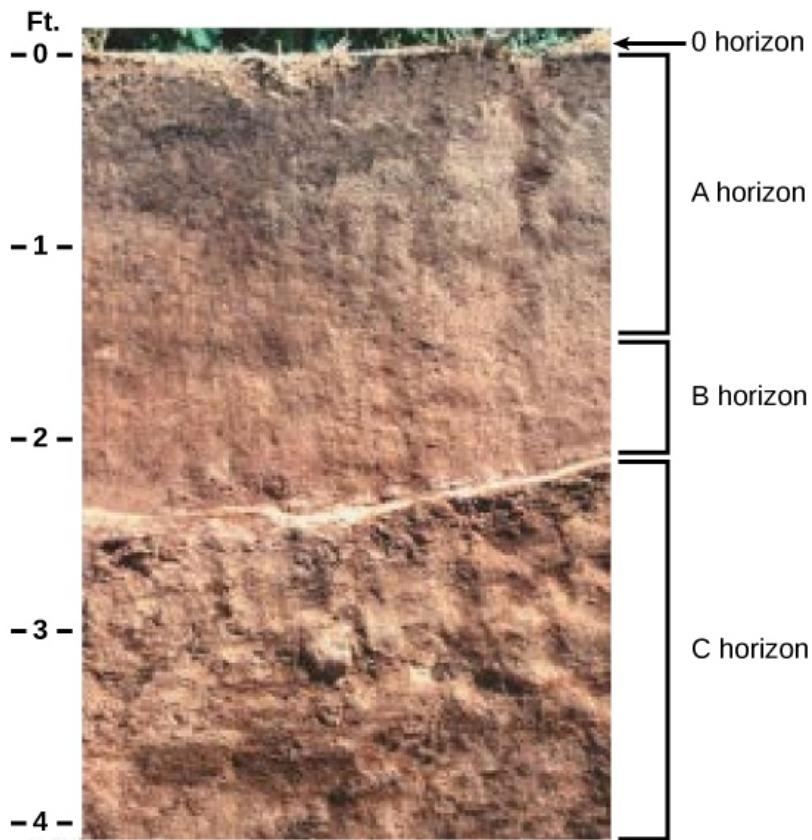
Art Connection

This soil profile shows the different soil layers (O horizon, A horizon, B horizon, and C horizon) found in typical soils. (credit: modification of work by USDA)



Which horizon is considered the topsoil, and which is considered the subsoil?

Some soils may have additional layers, or lack one of these layers. The thickness of the layers is also variable, and depends on the factors that influence soil formation. In general, immature soils may have O, A, and C horizons, whereas mature soils may display all of these, plus additional layers ([\[link\]](#)).



Career Connections Soil Scientist

A soil scientist studies the biological components, physical and chemical properties, distribution, formation, and morphology of soils. Soil scientists need to have a strong background in physical and life sciences, plus a foundation in mathematics. They may work for federal or state agencies, academia, or the private sector. Their work may involve collecting data, carrying out research,

interpreting results, inspecting soils, conducting soil surveys, and recommending soil management programs.

This soil scientist is studying the horizons and composition of soil at a research site. (credit: USDA)



Many soil scientists work both in an office and in the field. According to the United States Department of Agriculture (USDA): “a soil scientist needs good observation skills to analyze and

determine the characteristics of different types of soils. Soil types are complex and the geographical areas a soil scientist may survey are varied. Aerial photos or various satellite images are often used to research the areas. Computer skills and geographic information systems (GIS) help the scientist to analyze the multiple facets of geomorphology, topography, vegetation, and climate to discover the patterns left on the landscape.” [footnote] Soil scientists play a key role in understanding the soil’s past, analyzing present conditions, and making recommendations for future soil-related practices. National Resources Conservation Service / United States Department of Agriculture. “Careers in Soil Science.” <http://soils.usda.gov/education/facts/careers.html>

Section Summary

Plants obtain mineral nutrients from the soil. Soil is the outer loose layer that covers the surface of Earth. Soil quality depends on the chemical composition of the soil, the topography, the presence of living organisms, the climate, and time. Agricultural practice and history may also modify the characteristics and fertility of soil. Soil consists of four major components: 1) inorganic mineral

matter, 2) organic matter, 3) water and air, and 4) living matter. The organic material of soil is made of humus, which improves soil structure and provides water and minerals. Soil inorganic material consists of rock slowly broken down into smaller particles that vary in size, such as sand, silt, and loam.

Soil formation results from a combination of biological, physical, and chemical processes. Soil is not homogenous because its formation results in the production of layers called a soil profile. Factors that affect soil formation include: parent material, climate, topography, biological factors, and time. Soils are classified based on their horizons, soil particle size, and proportions. Most soils have four distinct horizons: O, A, B, and C.

Art Connections

[\[link\]](#) Soil compaction can result when soil is compressed by heavy machinery or even foot traffic. How might this compaction change the soil composition?

[\[link\]](#) The air content of the soil decreases.

[\[link\]](#) Which horizon is considered the topsoil,

and which is considered the subsoil?

[\[link\]](#) The A horizon is the topsoil, and the B horizon is subsoil.

Review Questions

Which factors affect soil quality?

1. chemical composition
 2. history of the soil
 3. presence of living organisms and topography
 4. all of the above
-

D

Soil particles that are 0.1 to 2 mm in diameter are called _____.

1. sand
 2. silt
 3. clay
 4. loam
-

A

A soil consists of layers called _____ that taken together are called a _____.

1. soil profiles : horizon
 2. horizons : soil profile
 3. horizons : humus
 4. humus : soil profile
-

B

What is the term used to describe the solid rock that lies beneath the soil?

1. sand
 2. bedrock
 3. clay
 4. loam
-

B

Describe the main differences between a mineral soil and an organic soil.

A mineral soil forms from the weathering of rocks; it is inorganic material. An organic soil is formed from sedimentation; it mostly consists of humus.

Name and briefly explain the factors that affect soil formation.

Parent material, climate, topography, biological factors, and time affect soil formation. Parent material is the material in which soils form. Climate describes how temperature, moisture, and wind cause different patterns of weathering, influencing the characteristics of the soil. Topography affects the characteristics and fertility of a soil. Biological factors include the presence of living organisms that greatly affect soil formation. Processes such as freezing and thawing may produce cracks in rocks; plant roots can penetrate these crevices and produce more fragmentation. Time affects soil because soil develops over long periods.

Describe how topography influences the characteristics and fertility of a soil.

Topography affects water runoff, which strips away parent material and affects plant growth.

Steeps soils are more prone to erosion and may be thinner than soils that are on level surfaces.

Glossary

A horizon

consists of a mixture of organic material with inorganic products of weathering

B horizon

soil layer that is an accumulation of mostly fine material that has moved downward

bedrock

solid rock that lies beneath the soil

C horizon

layer of soil that contains the parent material, and the organic and inorganic material that is broken down to form soil; also known as the soil base

clay

soil particles that are less than 0.002 mm in diameter

horizon

soil layer with distinct physical and chemical properties, which differs from other layers depending on how and when it was formed

humus

organic material of soil; made up of microorganisms, dead animals and plants in varying stages of decay

loam

soil that has no dominant particle size

mineral soil

type of soil that is formed from the weathering of rocks and inorganic material; composed primarily of sand, silt, and clay

O horizon

layer of soil with humus at the surface and decomposed vegetation at the base

organic soil

type of soil that is formed from sedimentation; composed primarily of organic material

parent material

organic and inorganic material in which soils form

rhizosphere

area of soil affected by root secretions and microorganisms

sand

soil particles between 0.1–2 mm in diameter

silt

soil particles between 0.002 and 0.1 mm in diameter

soil profile

vertical section of a soil

soil

outer loose layer that covers the surface of Earth

Transport of Water and Solutes in Plants

By the end of this section, you will be able to do the following:

- Define water potential and explain how it is influenced by solutes, pressure, gravity, and the matric potential
- Describe how water potential, evapotranspiration, and stomatal regulation influence how water is transported in plants
- Explain how photosynthates are transported in plants

The structure of plant roots, stems, and leaves facilitates the transport of water, nutrients, and photosynthates throughout the plant. The phloem and xylem are the main tissues responsible for this movement. Water potential, evapotranspiration, and stomatal regulation influence how water and nutrients are transported in plants. To understand how these processes work, we must first understand the energetics of water potential.

With heights nearing 116 meters, (a) coastal redwoods (*Sequoia sempervirens*) are the tallest trees in the world. Plant roots can easily generate enough force to (b) buckle and break concrete sidewalks, much to the dismay of homeowners and city maintenance departments. (credit a: modification of work by Bernt Rostad; credit b: modification of work by Pedestrians Educating Drivers on Safety, Inc.) When (a) total water potential (Ψ_{total}) is lower

outside the cells than inside, water moves out of the cells and the plant wilts. When (b) the total water potential is higher outside the plant cells than inside, water moves into the cells, resulting in turgor pressure (Ψ_p) and keeping the plant erect. (credit: modification of work by Victor M. Vicente Selvas)

Water Potential

Plants are phenomenal hydraulic engineers. Using only the basic laws of physics and the simple manipulation of potential energy, plants can move water to the top of a 116-meter-tall tree ([link]a). Plants can also use hydraulics to generate enough force to split rocks and buckle sidewalks ([link]b). Plants achieve this because of water potential.



(a)



(b)

Water potential is a measure of the potential energy in water. Plant physiologists are not interested in the energy in any one particular

aqueous system, but are very interested in water movement between two systems. In practical terms, therefore, water potential is the difference in potential energy between a given water sample and pure water (at atmospheric pressure and ambient temperature). Water potential is denoted by the Greek letter ψ (*psi*) and is expressed in units of pressure (pressure is a form of energy) called **megapascals (MPa)**. The potential of pure water ($\Psi_{\text{wpure H}_2\text{O}}$) is, by convenience of definition, designated a value of zero (even though pure water contains plenty of potential energy, that energy is ignored). Water potential values for the water in a plant root, stem, or leaf are therefore expressed relative to $\Psi_{\text{wpure H}_2\text{O}}$.

The water potential in plant solutions is influenced by solute concentration, pressure, gravity, and factors called matrix effects. Water potential can be broken down into its individual components using the following equation:

$$\Psi_{\text{system}} = \Psi_{\text{total}} = \Psi_s + \Psi_p + \Psi_g + \Psi_m$$

where Ψ_s , Ψ_p , Ψ_g , and Ψ_m refer to the solute, pressure, gravity, and matric potentials, respectively. “System” can refer to the water potential of the soil water (Ψ_{soil}), root water (Ψ_{root}), stem water (Ψ_{stem}), leaf water (Ψ_{leaf}) or the water in the atmosphere ($\Psi_{\text{atmosphere}}$): whichever aqueous system is under consideration. As the individual components change, they raise or lower the total

water potential of a system. When this happens, water moves to equilibrate, moving from the system or compartment with a higher water potential to the system or compartment with a lower water potential. This brings the difference in water potential between the two systems ($\Delta\Psi$) back to zero ($\Delta\Psi = 0$). Therefore, for water to move through the plant from the soil to the air (a process called transpiration), Ψ_{soil} must be $> \Psi_{\text{root}} > \Psi_{\text{stem}} > \Psi_{\text{leaf}} > \Psi_{\text{atmosphere}}$.

Water only moves in response to $\Delta\Psi$, not in response to the individual components. However, because the individual components influence the total Ψ_{system} , by manipulating the individual components (especially Ψ_s), a plant can control water movement.

Solute Potential

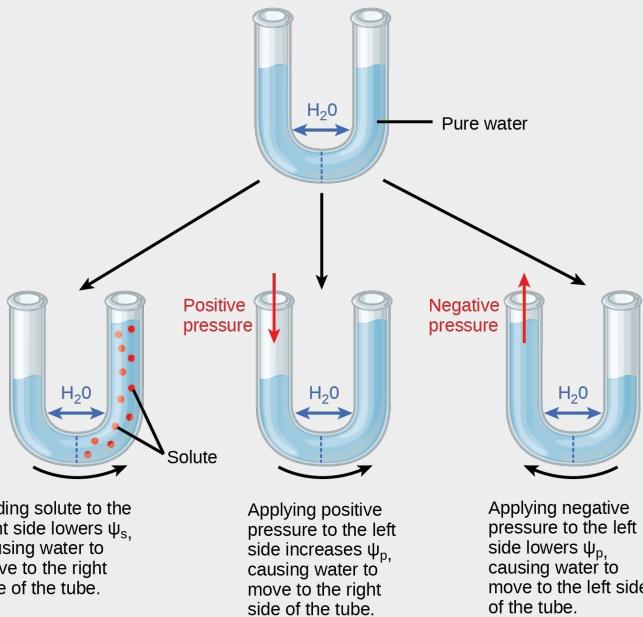
Solute potential (Ψ_s), also called osmotic potential, is related to the solute concentration (in molarity). That relationship is given by the van 't Hoff equation: $\Psi_s = -Mi RT$; where M is the molar concentration of the solute, i is the van 't Hoff factor (the ratio of the amount of particles in the solution to amount of formula units dissolved), R is the ideal gas constant, and T is temperature in Kelvin degrees. The solute potential is negative in a plant cell and zero in distilled water. Typical values for cell cytoplasm are -0.5 to -1.0 MPa. Solutes reduce

water potential (resulting in a negative Ψ_w) by consuming some of the potential energy available in the water. Solute molecules can dissolve in water because water molecules can bind to them via hydrogen bonds; a hydrophobic molecule like oil, which cannot bind to water, cannot go into solution. The energy in the hydrogen bonds between solute molecules and water is no longer available to do work in the system because it is tied up in the bond. In other words, the amount of available potential energy is reduced when solutes are added to an aqueous system. Thus, Ψ_s decreases with increasing solute concentration. Because Ψ_s is one of the four components of Ψ_{system} or Ψ_{total} , a decrease in Ψ_s will cause a decrease in Ψ_{total} . The internal water potential of a plant cell is more negative than pure water because of the cytoplasm's high solute content ([\[link\]](#)). Because of this difference in water potential water will move from the soil into a plant's root cells via the process of osmosis. This is why solute potential is sometimes called osmotic potential.

Plant cells can metabolically manipulate Ψ_s (and by extension, Ψ_{total}) by adding or removing solute molecules. Therefore, plants have control over Ψ_{total} via their ability to exert metabolic control over Ψ_s .

In this example with a semipermeable membrane between two aqueous systems, water will move

from a region of higher to lower water potential until equilibrium is reached. Solutes (Ψ_s), pressure (Ψ_p), and gravity (Ψ_g) influence total water potential for each side of the tube ($\Psi_{\text{total right or left}}$), and therefore, the difference between Ψ_{total} on each side ($\Delta\Psi$). (Ψ_m , the potential due to interaction of water with solid substrates, is ignored in this example because glass is not especially hydrophilic). Water moves in response to the difference in water potential between two systems (the left and right sides of the tube).



Positive water potential is placed on the left side of the tube by increasing Ψ_p such that the water level rises on the right side. Could you equalize the water level on each side of the tube by adding solute, and if so, how?

Pressure Potential

Pressure potential (Ψ_p), also called turgor potential, may be positive or negative ([\[link\]](#)). Because pressure is an expression of energy, the higher the pressure, the more potential energy in a system, and vice versa. Therefore, a positive Ψ_p (compression) increases Ψ_{total} , and a negative Ψ_p (tension) decreases Ψ_{total} . Positive pressure inside cells is contained by the cell wall, producing turgor pressure. Pressure potentials are typically around 0.6–0.8 MPa, but can reach as high as 1.5 MPa in a well-watered plant. A Ψ_p of 1.5 MPa equates to 210 pounds per square inch ($1.5 \text{ MPa} \times 140 \text{ lb/in}^{-2}$ MPa $^{-1}$ = 210 lb/in $^{-2}$). As a comparison, most automobile tires are kept at a pressure of 30–34 psi. An example of the effect of turgor pressure is the wilting of leaves and their restoration after the plant has been watered ([\[link\]](#)). Water is lost from the leaves via transpiration (approaching $\Psi_p = 0 \text{ MPa}$ at the wilting point) and restored by uptake via the roots.

A plant can manipulate Ψ_p via its ability to manipulate Ψ_s and by the process of osmosis. If a plant cell increases the cytoplasmic solute concentration, Ψ_s will decline, Ψ_{total} will decline, the $\Delta\Psi$ between the cell and the surrounding tissue will decline, water will move into the cell by osmosis, and Ψ_p will increase. Ψ_p is also under indirect plant control via the opening and closing of

stomata. Stomatal openings allow water to evaporate from the leaf, reducing Ψ_p and Ψ_{total} of the leaf and increasing Ψ between the water in the leaf and the petiole, thereby allowing water to flow from the petiole into the leaf.



(a)



(b)

Gravity Potential

Gravity potential (Ψ_g) is always negative to zero in a plant with no height. It always removes or consumes potential energy from the system. The force of gravity pulls water downwards to the soil, reducing the total amount of potential energy in the water in the plant (Ψ_{total}). The taller the plant, the taller the water column, and the more influential Ψ_g becomes. On a cellular scale and in short plants, this effect is negligible and easily ignored. However, over the height of a tall tree like a giant coastal redwood, the gravitational pull of -0.1 MPa m^{-1} is equivalent to an extra 1 MPa of resistance that must be overcome for water to reach the leaves of the tallest trees. Plants are unable to manipulate Ψ_g .

Matric Potential

Matric potential (Ψ_m) is always negative to zero. In a dry system, it can be as low as -2 MPa in a dry seed, and it is zero in a water-saturated system. The binding of water to a matrix always removes or consumes potential energy from the system. Ψ_m is similar to solute potential because it involves tying up the energy in an aqueous system by forming hydrogen bonds between the water and some other component. However, in solute potential, the other components are soluble, hydrophilic solute molecules, whereas in Ψ_m , the other components are insoluble, hydrophilic molecules of the plant cell wall. Every plant cell has a cellulosic cell wall and the cellulose in the cell walls is hydrophilic, producing a matrix for adhesion of water: hence the name matric potential. Ψ_m is very large (negative) in dry tissues such as seeds or drought-affected soils. However, it quickly goes to zero as the seed takes up water or the soil hydrates. Ψ_m cannot be manipulated by the plant and is typically ignored in well-watered roots, stems, and leaves.

Plants are suited to their local environment. (a) Xerophytes, like this prickly pear cactus (*Opuntia sp.*) and (b) epiphytes such as this tropical *Aeschynanthus perrottetii* have adapted to very limited water resources. The leaves of a prickly pear are modified into spines, which lowers the surface-to-volume ratio and reduces water loss.

Photosynthesis takes place in the stem, which also

stores water. (b) *A. perrottetii* leaves have a waxy cuticle that prevents water loss. (c) Goldenrod (*Solidago sp.*) is a mesophyte, well suited for moderate environments. (d) Hydrophytes, like this fragrant water lily (*Nymphaea odorata*), are adapted to thrive in aquatic environments. (credit a: modification of work by Jon Sullivan; credit b: modification of work by L. Shyamal/Wikimedia Commons; credit c: modification of work by Huw Williams; credit d: modification of work by Jason Hollinger)

Movement of Water and Minerals in the Xylem

Solutes, pressure, gravity, and matric potential are all important for the transport of water in plants. Water moves from an area of higher total water potential (higher Gibbs free energy) to an area of lower total water potential. Gibbs free energy is the energy associated with a chemical reaction that can be used to do work. This is expressed as $\Delta\Psi$.

Transpiration is the loss of water from the plant through evaporation at the leaf surface. It is the main driver of water movement in the xylem.

Transpiration is caused by the evaporation of water at the leaf–atmosphere interface; it creates negative pressure (tension) equivalent to -2 MPa at the leaf surface. This value varies greatly depending on the vapor pressure deficit, which can be negligible at

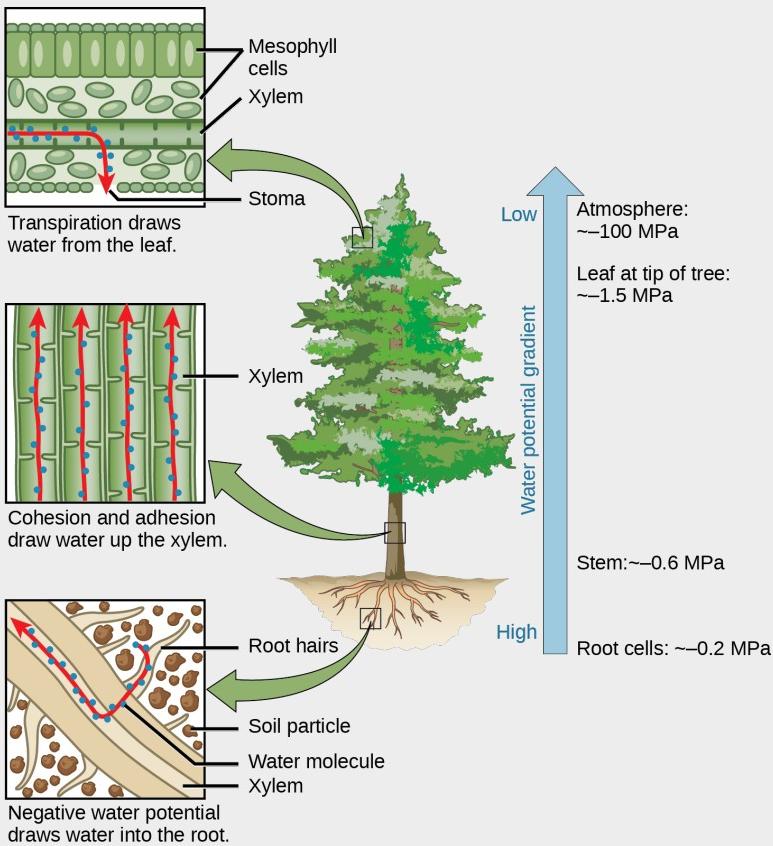
high relative humidity (RH) and substantial at low RH. Water from the roots is pulled up by this tension. At night, when stomata shut and transpiration stops, the water is held in the stem and leaf by the adhesion of water to the cell walls of the xylem vessels and tracheids, and the cohesion of water molecules to each other. This is called the cohesion–tension theory of sap ascent.

Inside the leaf at the cellular level, water on the surface of mesophyll cells saturates the cellulose microfibrils of the primary cell wall. The leaf contains many large intercellular air spaces for the exchange of oxygen for carbon dioxide, which is required for photosynthesis. The wet cell wall is exposed to this leaf internal air space, and the water on the surface of the cells evaporates into the air spaces, decreasing the thin film on the surface of the mesophyll cells. This decrease creates a greater tension on the water in the mesophyll cells ([\[link\]](#)), thereby increasing the pull on the water in the xylem vessels. The xylem vessels and tracheids are structurally adapted to cope with large changes in pressure. Rings in the vessels maintain their tubular shape, much like the rings on a vacuum cleaner hose keep the hose open while it is under pressure. Small perforations between vessel elements reduce the number and size of gas bubbles that can form via a process called cavitation. The formation of gas bubbles in xylem interrupts the continuous stream of water from the base to the top of the plant,

causing a break termed an embolism in the flow of xylem sap. The taller the tree, the greater the tension forces needed to pull water, and the more cavitation events. In larger trees, the resulting embolisms can plug xylem vessels, making them nonfunctional.

Visual Connection

The cohesion–tension theory of sap ascent is shown. Evaporation from the mesophyll cells produces a negative water potential gradient that causes water to move upwards from the roots through the xylem.



Which of the following statements is false?

1. Negative water potential draws water into the root hairs. Cohesion and adhesion draw water up the xylem. Transpiration draws water from the leaf.
2. Negative water potential draws water into the root hairs. Cohesion and adhesion draw water up the phloem. Transpiration draws water from the leaf.
3. Water potential decreases from the roots to the top of the plant.
4. Water enters the plants through root hairs and

exits through stoma.

Transpiration—the loss of water vapor to the atmosphere through stomata—is a passive process, meaning that metabolic energy in the form of ATP is not required for water movement. The energy driving transpiration is the difference in energy between the water in the soil and the water in the atmosphere. However, transpiration is tightly controlled.

Control of Transpiration

The atmosphere to which the leaf is exposed drives transpiration, but also causes massive water loss from the plant. Up to 90 percent of the water taken up by roots may be lost through transpiration.

Leaves are covered by a waxy **cuticle** on the outer surface that prevents the loss of water. Regulation of transpiration, therefore, is achieved primarily through the opening and closing of stomata on the leaf surface. Stomata are surrounded by two specialized cells called guard cells, which open and close in response to environmental cues such as light intensity and quality, leaf water status, and carbon dioxide concentrations. Stomata must open to allow air containing carbon dioxide and oxygen to diffuse into the leaf for photosynthesis and

respiration. When stomata are open, however, water vapor is lost to the external environment, increasing the rate of transpiration. Therefore, plants must maintain a balance between efficient photosynthesis and water loss.

Plants have evolved over time to adapt to their local environment and reduce transpiration ([\[link\]](#)). Desert plant (xerophytes) and plants that grow on other plants (epiphytes) have limited access to water. Such plants usually have a much thicker waxy cuticle than those growing in more moderate, well-watered environments (mesophytes). Aquatic plants (hydrophytes) also have their own set of anatomical and morphological leaf adaptations.



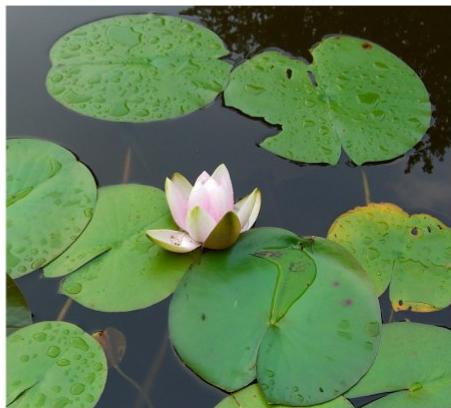
(a)



(b)



(c)



(d)

Xerophytes and epiphytes often have a thick covering of trichomes or of stomata that are sunken below the leaf's surface. Trichomes are specialized hair-like epidermal cells that secrete oils and substances. These adaptations impede air flow across the stomatal pore and reduce transpiration. Multiple epidermal layers are also commonly found

in these types of plants.

Phloem is comprised of cells called sieve-tube elements. Phloem sap travels through perforations called sieve tube plates. Neighboring companion cells carry out metabolic functions for the sieve-tube elements and provide them with energy. Lateral sieve areas connect the sieve-tube elements to the companion cells. Sucrose is actively transported from source cells into companion cells and then into the sieve-tube elements. This reduces the water potential, which causes water to enter the phloem from the xylem. The resulting positive pressure forces the sucrose-water mixture down toward the roots, where sucrose is unloaded. Transpiration causes water to return to the leaves through the xylem vessels.

Transportation of Photosynthates in the Phloem

Plants need an energy source to grow. In seeds and bulbs, food is stored in polymers (such as starch) that are converted by metabolic processes into sucrose for newly developing plants. Once green shoots and leaves are growing, plants are able to produce their own food by photosynthesizing. The products of photosynthesis are called photosynthates, which are usually in the form of simple sugars such as sucrose.

Structures that produce photosynthates for the

growing plant are referred to as **sources**. Sugars produced in sources, such as leaves, need to be delivered to growing parts of the plant via the phloem in a process called **translocation**. The points of sugar delivery, such as roots, young shoots, and developing seeds, are called **sinks**. Seeds, tubers, and bulbs can be either a source or a sink, depending on the plant's stage of development and the season.

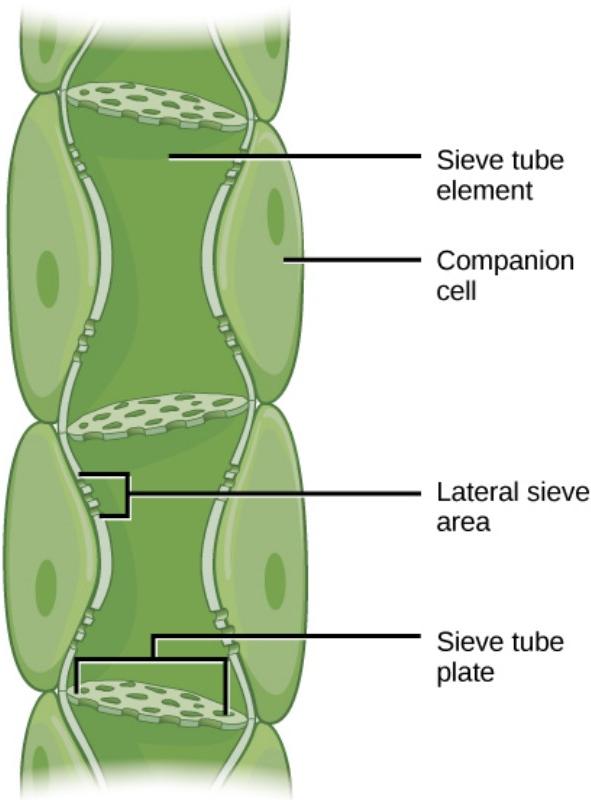
The products from the source are usually translocated to the nearest sink through the phloem. For example, the highest leaves will send photosynthates upward to the growing shoot tip, whereas lower leaves will direct photosynthates downward to the roots. Intermediate leaves will send products in both directions, unlike the flow in the xylem, which is always unidirectional (soil to leaf to atmosphere). The pattern of photosynthetic flow changes as the plant grows and develops. Photosynthates are directed primarily to the roots early on, to shoots and leaves during vegetative growth, and to seeds and fruits during reproductive development. They are also directed to tubers for storage.

Translocation: Transport from Source to Sink

Photosynthates, such as sucrose, are produced in the mesophyll cells of photosynthesizing leaves. From there they are translocated through the phloem to

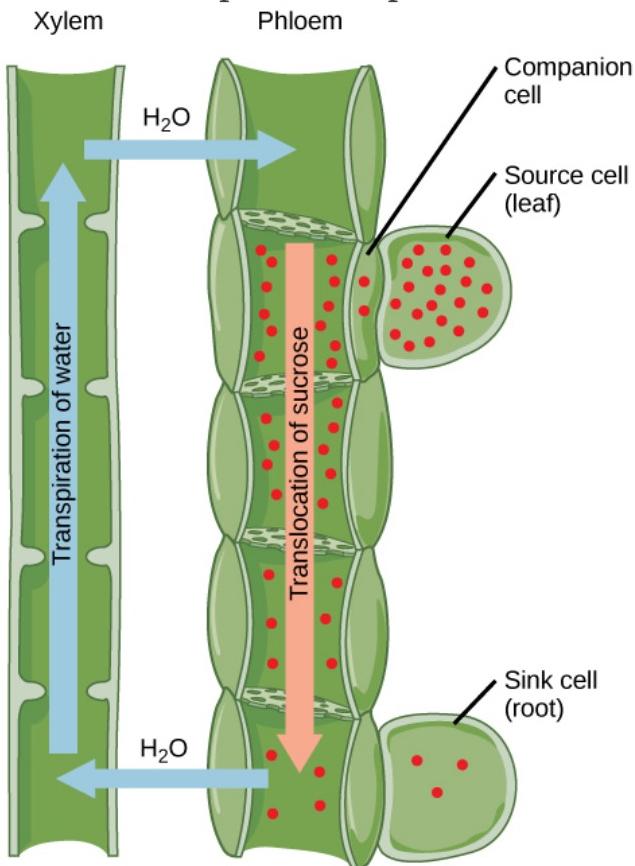
where they are used or stored. Mesophyll cells are connected by cytoplasmic channels called plasmodesmata. Photosynthates move through these channels to reach phloem sieve-tube elements (STEs) in the vascular bundles. From the mesophyll cells, the photosynthates are loaded into the phloem STEs. The sucrose is actively transported against its concentration gradient (a process requiring ATP) into the phloem cells using the electrochemical potential of the proton gradient. This is coupled to the uptake of sucrose with a carrier protein called the sucrose-H⁺ symporter.

Phloem STEs have reduced cytoplasmic contents, and are connected by a sieve plate with pores that allow for pressure-driven bulk flow, or translocation, of phloem sap. Companion cells are associated with STEs. They assist with metabolic activities and produce energy for the STEs ([\[link\]](#)).



Once in the phloem, the photosynthates are translocated to the closest sink. Phloem sap is an aqueous solution that contains up to 30 percent sugar, minerals, amino acids, and plant growth regulators. The high percentage of sugar decreases Ψ_s , which decreases the total water potential and causes water to move by osmosis from the adjacent xylem into the phloem tubes, thereby increasing pressure. This increase in total water potential causes the bulk flow of phloem from source to sink ([\[link\]](#)). Sucrose concentration in the sink cells is lower than in the phloem STEs because the sink

sucrose has been metabolized for growth, or converted to starch for storage or other polymers, such as cellulose, for structural integrity. Unloading at the sink end of the phloem tube occurs by either diffusion or active transport of sucrose molecules from an area of high concentration to one of low concentration. Water diffuses from the phloem by osmosis and is then transpired or recycled via the xylem back into the phloem sap.



Section Summary

Water potential (Ψ) is a measure of the difference in potential energy between a water sample and pure water. The water potential in plant solutions is influenced by solute concentration, pressure, gravity, and matric potential. Water potential and transpiration influence how water is transported through the xylem in plants. These processes are regulated by stomatal opening and closing.

Photosynthates (mainly sucrose) move from sources to sinks through the plant's phloem. Sucrose is actively loaded into the sieve-tube elements of the phloem. The increased solute concentration causes water to move by osmosis from the xylem into the phloem. The positive pressure that is produced pushes water and solutes down the pressure gradient. The sucrose is unloaded into the sink, and the water returns to the xylem vessels.

Visual Connection Questions

[\[link\]](#) Positive water potential is placed on the left side of the tube by increasing Ψ_p such that the water level rises on the right side. Could you equalize the water level on each side of the tube by adding solute, and if so, how?

[\[link\]](#) Yes, you can equalize the water level by adding the solute to the left side of the tube such that water moves toward the left until the water levels are equal.

[\[link\]](#) Which of the following statements is false?

1. Negative water potential draws water into the root hairs. Cohesion and adhesion draw water up the xylem. Transpiration draws water from the leaf.
2. Negative water potential draws water into the root hairs. Cohesion and adhesion draw water up the phloem. Transpiration draws water from the leaf.
3. Water potential decreases from the roots to the top of the plant.
4. Water enters the plants through root hairs and exits through stoma.

[\[link\]](#) B.

Review Questions

When stomata open, what occurs?

-
1. Water vapor is lost to the external environment, increasing the rate of transpiration.
 2. Water vapor is lost to the external environment, decreasing the rate of transpiration.
 3. Water vapor enters the spaces in the mesophyll, increasing the rate of transpiration.
 4. Water vapor enters the spaces in the mesophyll, decreasing the rate of transpiration.
-

A

Which cells are responsible for the movement of photosynthates through a plant?

1. tracheids, vessel elements
 2. tracheids, companion cells
 3. vessel elements, companion cells
 4. sieve-tube elements, companion cells
-

D

Critical Thinking Questions

The process of bulk flow transports fluids in a plant. Describe the two main bulk flow processes.

The process of bulk flow moves water up the xylem and moves photosynthates (solutes) up and down the phloem.

Glossary

cuticle

waxy covering on the outside of the leaf and stem that prevents the loss of water

megapascal (MPa)

pressure units that measure water potential

sink

growing parts of a plant, such as roots and young leaves, which require photosynthate

source

organ that produces photosynthate for a plant

translocation

mass transport of photosynthates from source to sink in vascular plants

transpiration

loss of water vapor to the atmosphere through

stomata

water potential (Ψ_w)

the potential energy of a water solution per unit volume in relation to pure water at atmospheric pressure and ambient temperature

Animal Form and Function

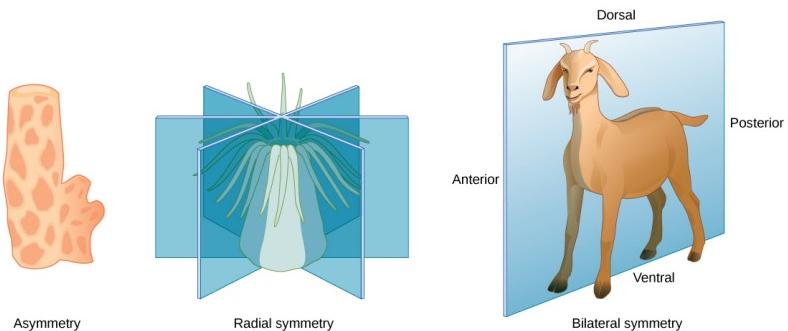
By the end of this section, you will be able to:

- Describe the various types of body plans that occur in animals
- Describe limits on animal size and shape
- Relate bioenergetics to body size, levels of activity, and the environment

Animals vary in form and function. From a sponge to a worm to a goat, an organism has a distinct body plan that limits its size and shape. Animals' bodies are also designed to interact with their environments, whether in the deep sea, a rainforest canopy, or the desert. Therefore, a large amount of information about the structure of an organism's body (anatomy) and the function of its cells, tissues and organs (physiology) can be learned by studying that organism's environment.

Animals exhibit different types of body symmetry. The sponge is asymmetrical, the sea anemone has radial symmetry, and the goat has bilateral symmetry.

Body Plans



Animal body plans follow set patterns related to symmetry. They are asymmetrical, radial, or bilateral in form as illustrated in [\[link\]](#).

Asymmetrical animals are animals with no pattern or symmetry; an example of an asymmetrical animal is a sponge. Radial symmetry, as illustrated in [\[link\]](#), describes when an animal has an up-and-down orientation: any plane cut along its longitudinal axis through the organism produces equal halves, but not a definite right or left side. This plan is found mostly in aquatic animals, especially organisms that attach themselves to a base, like a rock or a boat, and extract their food from the surrounding water as it flows around the organism. Bilateral symmetry is illustrated in the same figure by a goat. The goat also has an upper and lower component to it, but a plane cut from front to back separates the animal into definite right and left sides. Additional terms used when describing positions in the body are anterior (front), posterior (rear), dorsal (toward the back), and ventral (toward the stomach). Bilateral symmetry is found in both land-based and aquatic animals; it

enables a high level of mobility.

Apodemes are ingrowths on arthropod exoskeletons to which muscles attach. The apodemes on this crab leg are located above and below the fulcrum of the claw. Contraction of muscles attached to the apodemes pulls the claw closed.

Limits on Animal Size and Shape

Animals with bilateral symmetry that live in water tend to have a **fusiform** shape: this is a tubular shaped body that is tapered at both ends. This shape decreases the drag on the body as it moves through water and allows the animal to swim at high speeds. [\[link\]](#) lists the maximum speed of various animals. Certain types of sharks can swim at fifty kilometers an hour and some dolphins at 32 to 40 kilometers per hour. Land animals frequently travel faster, although the tortoise and snail are significantly slower than cheetahs. Another difference in the adaptations of aquatic and land-dwelling organisms is that aquatic organisms are constrained in shape by the forces of drag in the water since water has higher viscosity than air. On the other hand, land-dwelling organisms are constrained mainly by gravity, and drag is relatively unimportant. For example, most adaptations in birds are for gravity not for drag.

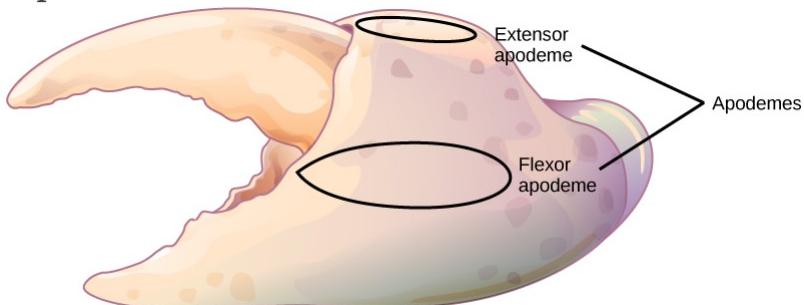
Maximum Speed of Assorted Land Marine Animals

Animal	Speed (kmh)	Speed (mph)
Cheetah	113	70
Quarter horse	77	48
Fox	68	42
Shortfin mako shark	50	31
Domestic house cat	48	30
Human	45	28
Dolphin	32 - 40	20 - 25
Mouse	13	8
Snail	0.05	0.03

Most animals have an exoskeleton, including insects, spiders, scorpions, horseshoe crabs, centipedes, and crustaceans. Scientists estimate that, of insects alone, there are over 30 million species on our planet. The exoskeleton is a hard covering or shell that provides benefits to the animal, such as protection against damage from predators and from water loss (for land animals); it also provides for the attachments of muscles.

As the tough and resistant outer cover of an arthropod, the exoskeleton may be constructed of a tough polymer such as chitin and is often biomineralized with materials such as calcium

carbonate. This is fused to the animal's epidermis. Ingrowths of the exoskeleton, called **apodemes**, function as attachment sites for muscles, similar to tendons in more advanced animals ([\[link\]](#)). In order to grow, the animal must first synthesize a new exoskeleton underneath the old one and then shed or molt the original covering. This limits the animal's ability to grow continually, and may limit the individual's ability to mature if molting does not occur at the proper time. The thickness of the exoskeleton must be increased significantly to accommodate any increase in weight. It is estimated that a doubling of body size increases body weight by a factor of eight. The increasing thickness of the chitin necessary to support this weight limits most animals with an exoskeleton to a relatively small size. The same principles apply to endoskeletons, but they are more efficient because muscles are attached on the outside, making it easier to compensate for increased mass.



An animal with an endoskeleton has its size determined by the amount of skeletal system it needs in order to support the other tissues and the

amount of muscle it needs for movement. As the body size increases, both bone and muscle mass increase. The speed achievable by the animal is a balance between its overall size and the bone and muscle that provide support and movement.

Limiting Effects of Diffusion on Size and Development

The exchange of nutrients and wastes between a cell and its watery environment occurs through the process of diffusion. All living cells are bathed in liquid, whether they are in a single-celled organism or a multicellular one. Diffusion is effective over a specific distance and limits the size that an individual cell can attain. If a cell is a single-celled microorganism, such as an amoeba, it can satisfy all of its nutrient and waste needs through diffusion. If the cell is too large, then diffusion is ineffective and the center of the cell does not receive adequate nutrients nor is it able to effectively dispel its waste.

An important concept in understanding how efficient diffusion is as a means of transport is the surface to volume ratio. Recall that any three-dimensional object has a surface area and volume; the ratio of these two quantities is the surface-to-volume ratio. Consider a cell shaped like a perfect sphere: it has a surface area of $4\pi r^2$, and a volume of $(4/3)\pi r^3$. The surface-to-volume ratio of a sphere

is $3/r$; as the cell gets bigger, its surface to volume ratio decreases, making diffusion less efficient. The larger the size of the sphere, or animal, the less surface area for diffusion it possesses.

The solution to producing larger organisms is for them to become multicellular. Specialization occurs in complex organisms, allowing cells to become more efficient at doing fewer tasks. For example, circulatory systems bring nutrients and remove waste, while respiratory systems provide oxygen for the cells and remove carbon dioxide from them. Other organ systems have developed further specialization of cells and tissues and efficiently control body functions. Moreover, surface-to-volume ratio applies to other areas of animal development, such as the relationship between muscle mass and cross-sectional surface area in supporting skeletons, and in the relationship between muscle mass and the generation of dissipation of heat.

Link to Learning



Visit [this interactive site](#) to see an entire animal (a zebrafish embryo) at the cellular and sub-cellular level. Use the zoom and navigation functions for a virtual nanoscopy exploration.

The mouse has a much higher metabolic rate than the elephant. (credit “mouse”: modification of work by Magnus Kjaergaard; credit “elephant”: modification of work by “TheLizardQueen”/Flickr)

Animal Bioenergetics

All animals must obtain their energy from food they ingest or absorb. These nutrients are converted to adenosine triphosphate (ATP) for short-term storage and use by all cells. Some animals store energy for slightly longer times as glycogen, and others store energy for much longer times in the form of triglycerides housed in specialized adipose tissues. No energy system is one hundred percent efficient, and an animal’s metabolism produces waste energy in the form of heat. If an animal can conserve that heat and maintain a relatively constant body temperature, it is classified as a warm-blooded animal and called an **endotherm**. The insulation used to conserve the body heat comes in the forms of fur, fat, or feathers. The absence of insulation in **ectothermic** animals increases their dependence on the environment for body heat.

The amount of energy expended by an animal over a specific time is called its metabolic rate. The rate is measured variously in joules, calories, or kilocalories (1000 calories). Carbohydrates and proteins contain about 4.5 to 5 kcal/g, and fat contains about 9 kcal/g. Metabolic rate is estimated as the **basal metabolic rate (BMR)** in endothermic animals at rest and as the **standard metabolic rate (SMR)** in ectotherms. Human males have a BMR of 1600 to 1800 kcal/day, and human females have a BMR of 1300 to 1500 kcal/day. Even with insulation, endothermal animals require extensive amounts of energy to maintain a constant body temperature. An ectotherm such as an alligator has an SMR of 60 kcal/day.

Energy Requirements Related to Body Size

Smaller endothermic animals have a greater surface area for their mass than larger ones ([\[link\]](#)). Therefore, smaller animals lose heat at a faster rate than larger animals and require more energy to maintain a constant internal temperature. This results in a smaller endothermic animal having a higher BMR, per body weight, than a larger endothermic animal.

Species		
Mass	35 g	4,500,000 g
Metabolic rate	$890 \text{ mm}^3 \text{ O}_2/\text{g body mass/hr}$	$75 \text{ mm}^3 \text{ O}_2/\text{g body mass/hr}$

Energy Requirements Related to Levels of Activity

The more active an animal is, the more energy is needed to maintain that activity, and the higher its BMR or SMR. The average daily rate of energy consumption is about two to four times an animal's BMR or SMR. Humans are more sedentary than most animals and have an average daily rate of only 1.5 times the BMR. The diet of an endothermic animal is determined by its BMR. For example: the type of grasses, leaves, or shrubs that an herbivore eats affects the number of calories that it takes in. The relative caloric content of herbivore foods, in descending order, is tall grasses > legumes > short grasses > forbs (any broad-leaved plant, not a grass) > subshrubs > annuals/biennials.

Energy Requirements Related to Environment

Animals adapt to extremes of temperature or food availability through torpor. **Torpor** is a process that leads to a decrease in activity and metabolism and

allows animals to survive adverse conditions. Torpor can be used by animals for long periods, such as entering a state of **hibernation** during the winter months, in which case it enables them to maintain a reduced body temperature. During hibernation, ground squirrels can achieve an abdominal temperature of 0° C (32° F), while a bear's internal temperature is maintained higher at about 37° C (99° F).

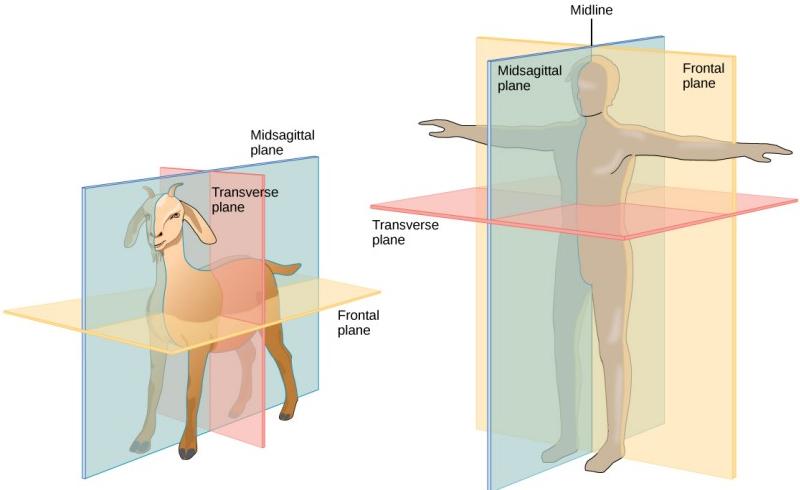
If torpor occurs during the summer months with high temperatures and little water, it is called **estivation**. Some desert animals use this to survive the harshest months of the year. Torpor can occur on a daily basis; this is seen in bats and hummingbirds. While endothermy is limited in smaller animals by surface to volume ratio, some organisms can be smaller and still be endotherms because they employ daily torpor during the part of the day that is coldest. This allows them to conserve energy during the colder parts of the day, when they consume more energy to maintain their body temperature.

Shown are the planes of a quadruped goat and a bipedal human. The midsagittal plane divides the body exactly in half, into right and left portions. The frontal plane divides the front and back, and the transverse plane divides the body into upper and lower portions. Vertebrate animals have two major body cavities. The dorsal cavity, indicated in green, contains the cranial and the spinal cavity. The

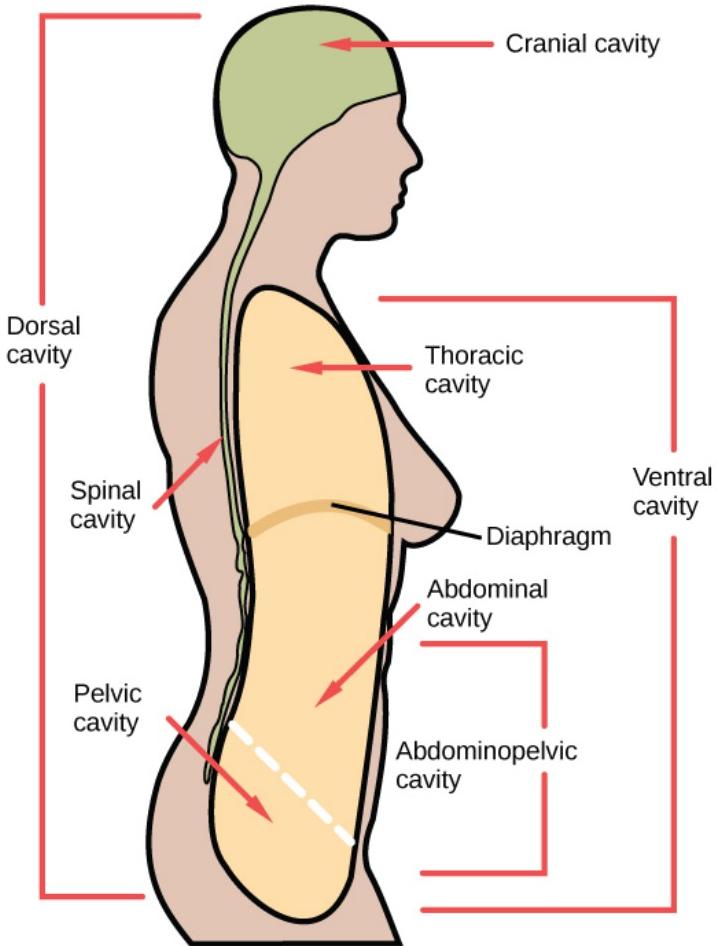
ventral cavity, indicated in yellow, contains the thoracic cavity and the abdominopelvic cavity. The thoracic cavity is separated from the abdominopelvic cavity by the diaphragm. The thoracic cavity is separated into the abdominal cavity and the pelvic cavity by an imaginary line parallel to the pelvis bones. (credit: modification of work by NCI)

Animal Body Planes and Cavities

A standing vertebrate animal can be divided by several planes. A **sagittal plane** divides the body into right and left portions. A **midsagittal plane** divides the body exactly in the middle, making two equal right and left halves. A **frontal plane** (also called a coronal plane) separates the front from the back. A **transverse plane** (or, horizontal plane) divides the animal into upper and lower portions. This is sometimes called a cross section, and, if the transverse cut is at an angle, it is called an oblique plane. [\[link\]](#) illustrates these planes on a goat (a four-legged animal) and a human being.



Vertebrate animals have a number of defined body cavities, as illustrated in [\[link\]](#). Two of these are major cavities that contain smaller cavities within them. The **dorsal cavity** contains the cranial and the vertebral (or spinal) cavities. The **ventral cavity** contains the thoracic cavity, which in turn contains the pleural cavity around the lungs and the pericardial cavity, which surrounds the heart. The ventral cavity also contains the abdominopelvic cavity, which can be separated into the abdominal and the pelvic cavities.



Career Connections

Physical Anthropologist

Physical anthropologists study the adaption, variability, and evolution of human beings, plus their living and fossil relatives. They can work in a variety of settings, although most will have an academic appointment at a university, usually in

an anthropology department or a biology, genetics, or zoology department.

Non-academic positions are available in the automotive and aerospace industries where the focus is on human size, shape, and anatomy. Research by these professionals might range from studies of how the human body reacts to car crashes to exploring how to make seats more comfortable. Other non-academic positions can be obtained in museums of natural history, anthropology, archaeology, or science and technology. These positions involve educating students from grade school through graduate school. Physical anthropologists serve as education coordinators, collection managers, writers for museum publications, and as administrators. Zoos employ these professionals, especially if they have an expertise in primate biology; they work in collection management and captive breeding programs for endangered species. Forensic science utilizes physical anthropology expertise in identifying human and animal remains, assisting in determining the cause of death, and for expert testimony in trials.

Section Summary

Animal bodies come in a variety of sizes and shapes. Limits on animal size and shape include impacts to their movement. Diffusion affects their size and development. Bioenergetics describes how animals use and obtain energy in relation to their body size, activity level, and environment.

Review Questions

Which type of animal maintains a constant internal body temperature?

1. endotherm
 2. ectotherm
 3. coelomate
 4. mesoderm
-

A

The symmetry found in animals that move swiftly is _____.

1. radial
2. bilateral
3. sequential
4. interrupted

B

What term describes the condition of a desert mouse that lowers its metabolic rate and “sleeps” during the hot day?

1. turgid
 2. hibernation
 3. estivation
 4. normal sleep pattern
-

C

A plane that divides an animal into equal right and left portions is ____.

1. diagonal
 2. midsagittal
 3. coronal
 4. transverse
-

B

A plane that divides an animal into dorsal and ventral portions is ____.

1. sagittal

-
- 2. midsagittal
 - 3. coronal
 - 4. transverse
-

D

The pleural cavity is a part of which cavity?

- 1. dorsal cavity
 - 2. thoracic cavity
 - 3. abdominal cavity
 - 4. pericardial cavity
-

B

Free Response

How does diffusion limit the size of an organism? How is this counteracted?

Diffusion is effective over a very short distance. If a cell exceeds this distance in its size, the center of the cell cannot get adequate nutrients nor can it expel enough waste to survive. To compensate for this, cells can loosely adhere to

each other in a liquid medium, or develop into multi-celled organisms that use circulatory and respiratory systems to deliver nutrients and remove wastes.

What is the relationship between BMR and body size? Why?

Basal Metabolic Rate is an expression of the metabolic processes that occur to maintain an individual's functioning and body temperature. Smaller bodied animals have a relatively large surface area compared to a much larger animal. The small animal's large surface area leads to increased heat loss that the animal must compensate for, resulting in a higher BMR. A large animal, having less relative surface area, does not lose as much heat and has a correspondingly lower BMR.

Glossary

apodeme

ingrowth of an animal's exoskeleton that functions as an attachment site for muscles

asymmetrical

describes animals with no axis of symmetry in their body pattern

basal metabolic rate (BMR)

metabolic rate at rest in endothermic animals

dorsal cavity

body cavity on the posterior or back portion of an animal; includes the cranial and vertebral cavities

ectotherm

animal incapable of maintaining a relatively constant internal body temperature

endotherm

animal capable of maintaining a relatively constant internal body temperature

estivation

torpor in response to extremely high temperatures and low water availability

frontal (coronal) plane

plane cutting through an animal separating the individual into front and back portions

fusiform

animal body shape that is tubular and tapered at both ends

hibernation

torpor over a long period of time, such as a winter

midsagittal plane

plane cutting through an animal separating the individual into even right and left sides

sagittal plane

plane cutting through an animal separating the individual into right and left sides

standard metabolic rate (SMR)

metabolic rate at rest in ectothermic animals

torpor

decrease in activity and metabolism that allows an animal to survive adverse conditions

transverse (horizontal) plane

plane cutting through an animal separating the individual into upper and lower portions

ventral cavity

body cavity on the anterior or front portion of an animal that includes the thoracic cavities and the abdominopelvic cavities

Animal Primary Tissues

By the end of this section, you will be able to do the following:

- Describe epithelial tissues
- Discuss the different types of connective tissues in animals
- Describe three types of muscle tissues
- Describe nervous tissue

The tissues of multicellular, complex animals are four primary types: epithelial, connective, muscle, and nervous. Recall that tissues are groups of similar cells (cells carrying out related functions). These tissues combine to form organs—like the skin or kidney—that have specific, specialized functions within the body. Organs are organized into organ systems to perform functions; examples include the circulatory system, which consists of the heart and blood vessels, and the digestive system, consisting of several organs, including the stomach, intestines, liver, and pancreas. Organ systems come together to create an entire organism.

Squamous epithelia cells (a) have a slightly irregular shape, and a small, centrally located nucleus. These cells can be stratified into layers, as in (b) this human cervix specimen. (credit b: modification of work by Ed Uthman; scale-bar data from Matt Russell) Simple cuboidal epithelial cells line tubules in the mammalian kidney, where they are involved in filtering the blood. Simple columnar

epithelial cells absorb material from the digestive tract. Goblet cells secrete mucus into the digestive tract lumen. Pseudostratified columnar epithelia line the respiratory tract. They exist in one layer, but the arrangement of nuclei at different levels makes it appear that there is more than one layer. Goblet cells interspersed between the columnar epithelial cells secrete mucus into the respiratory tract.

Epithelial Tissues

Epithelial tissues cover the outside of organs and structures in the body and line the lumens of organs in a single layer or multiple layers of cells. The types of epithelia are classified by the shapes of cells present and the number of layers of cells. Epithelia composed of a single layer of cells is called **simple epithelia**; epithelial tissue composed of multiple layers is called **stratified epithelia**. [\[link\]](#) summarizes the different types of epithelial tissues.

Different Types of Epithelial

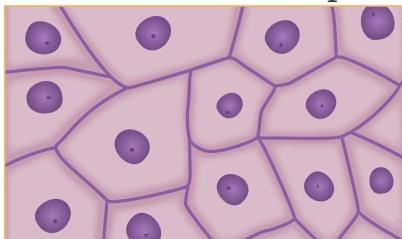
Tissues

Cell shape	Description	Location
squamous	flat, irregular	simple: lung

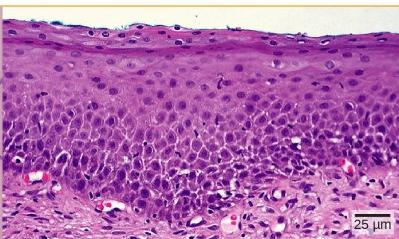
	round shape	alveoli, capillaries; stratified: skin, mouth, vagina glands, renal tubules
cuboidal	cube shaped, central nucleus	
columnar	tall, narrow, nucleus toward base; tall, narrow, nucleus along cell	simple: digestive tract; pseudostratified: respiratory tract
transitional	round, simple but appear stratified	urinary bladder

Squamous Epithelia

Squamous epithelial cells are generally round, flat, and have a small, centrally located nucleus. The cell outline is slightly irregular, and cells fit together to form a covering or lining. When the cells are arranged in a single layer (simple epithelia), they facilitate diffusion in tissues, such as the areas of gas exchange in the lungs and the exchange of nutrients and waste at blood capillaries.



(a)

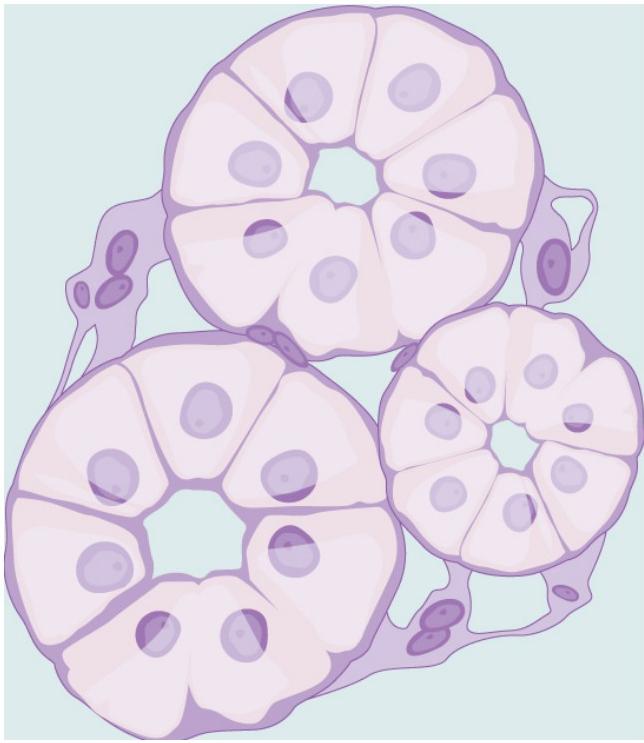


(b)

[\[link\]a](#) illustrates a layer of squamous cells with their membranes joined together to form an epithelium. Image [\[link\]b](#) illustrates squamous epithelial cells arranged in stratified layers, where protection is needed on the body from outside abrasion and damage. This is called a stratified squamous epithelium and occurs in the skin and in tissues lining the mouth and vagina.

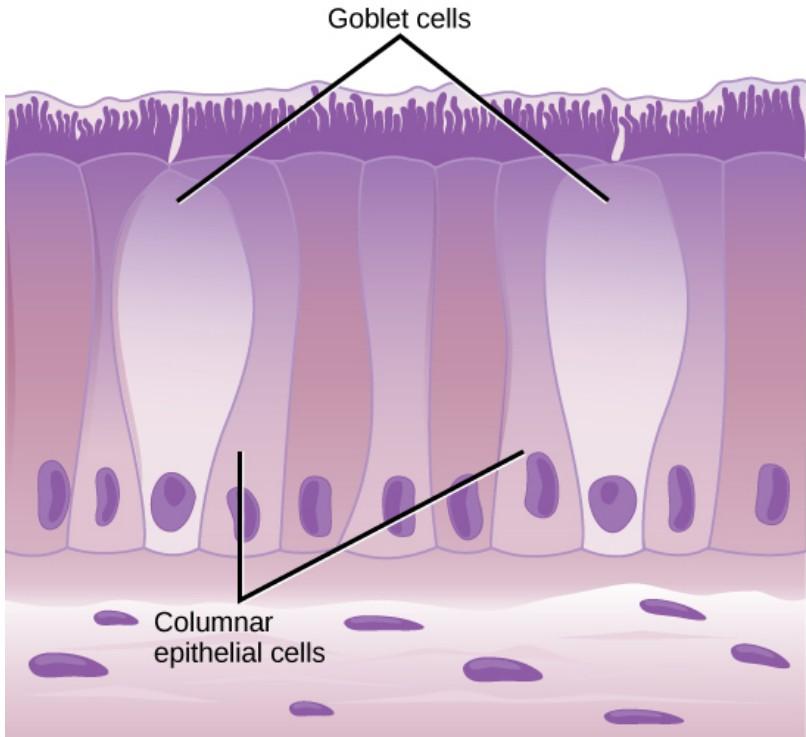
Cuboidal Epithelia

Cuboidal epithelial cells, shown in [\[link\]](#), are cube-shaped with a single, central nucleus. They are most commonly found in a single layer representing a simple epithelia in glandular tissues throughout the body where they prepare and secrete glandular material. They are also found in the walls of tubules and in the ducts of the kidney and liver.



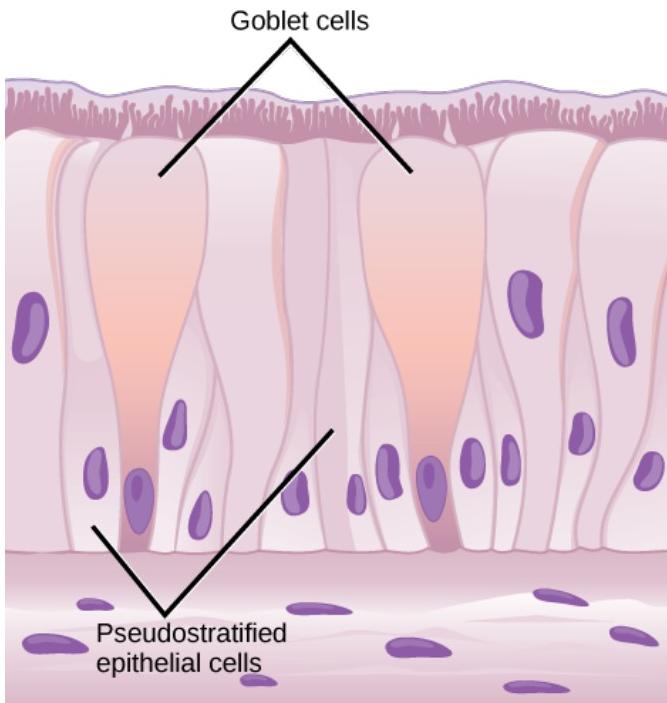
Columnar Epithelia

Columnar epithelial cells are taller than they are wide: they resemble a stack of columns in an epithelial layer, and are most commonly found in a single-layer arrangement. The nuclei of columnar epithelial cells in the digestive tract appear to be lined up at the base of the cells, as illustrated in [\[link\]](#). These cells absorb material from the lumen of the digestive tract and prepare it for entry into the body through the circulatory and lymphatic systems.



Columnar epithelial cells lining the respiratory tract appear to be stratified. However, each cell is attached to the base membrane of the tissue and, therefore, they are simple tissues. The nuclei are arranged at different levels in the layer of cells, making it appear as though there is more than one layer, as seen in [\[link\]](#). This is called **pseudostratified**, columnar epithelia. This cellular covering has cilia at the apical, or free, surface of the cells. The cilia enhance the movement of mucus and trapped particles out of the respiratory tract, helping to protect the system from invasive microorganisms and harmful material that has been

breathed into the body. Goblet cells are interspersed in some tissues (such as the lining of the trachea). The goblet cells contain mucus that traps irritants, which in the case of the trachea keep these irritants from getting into the lungs.



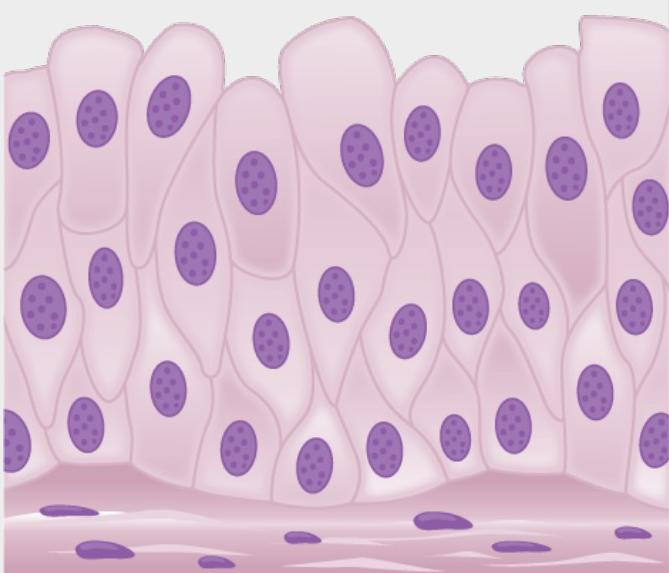
Transitional Epithelia

Transitional or uroepithelial cells appear only in the urinary system, primarily in the bladder and ureter. These cells are arranged in a stratified layer, but they have the capability of appearing to pile up on top of each other in a relaxed, empty bladder, as illustrated in [\[link\]](#). As the urinary bladder fills, the epithelial layer unfolds and expands to hold the

volume of urine introduced into it. As the bladder fills, it expands and the lining becomes thinner. In other words, the tissue transitions from thick to thin.

Visual Connection

Transitional epithelia of the urinary bladder undergo changes in thickness depending on how full the bladder is.



Which of the following statements about types of epithelial cells is false?

1. Simple columnar epithelial cells line the tissue of the lung.
2. Simple cuboidal epithelial cells are involved in

the filtering of blood in the kidney.

3. Pseudostratified columnar epithelia occur in a single layer, but the arrangement of nuclei makes it appear that more than one layer is present.
4. Transitional epithelia change in thickness depending on how full the bladder is.

Loose connective tissue is composed of loosely woven collagen and elastic fibers. The fibers and other components of the connective tissue matrix are secreted by fibroblasts. Fibrous connective tissue from the tendon has strands of collagen fibers lined up in parallel. Hyaline cartilage consists of a matrix with cells called chondrocytes embedded in it. The chondrocytes exist in cavities in the matrix called lacunae. (a) Compact bone is a dense matrix on the outer surface of bone. Spongy bone, inside the compact bone, is porous with web-like trabeculae. (b) Compact bone is organized into rings called osteons. Blood vessels, nerves, and lymphatic vessels are found in the central Haversian canal. Rings of lamellae surround the Haversian canal. Between the lamellae are cavities called lacunae. Canaliculi are microchannels connecting the lacunae together. (c) Osteoblasts surround the exterior of the bone. Osteoclasts bore tunnels into the bone and osteocytes are found in the lacunae. Adipose is a connective tissue made up of cells called

adipocytes. Adipocytes have small nuclei localized at the cell edge. Blood is a connective tissue that has a fluid matrix, called plasma, and no fibers.

Erythrocytes (red blood cells), the predominant cell type, are involved in the transport of oxygen and carbon dioxide. Also present are various leukocytes (white blood cells) involved in immune response.

Connective Tissues

Connective tissues are made up of a matrix consisting of living cells and a nonliving substance, called the ground substance. The ground substance is made of an organic substance (usually a protein) and an inorganic substance (usually a mineral or water). The principal cell of connective tissues is the fibroblast. This cell makes the fibers found in nearly all of the connective tissues. Fibroblasts are motile, able to carry out mitosis, and can synthesize whichever connective tissue is needed.

Macrophages, lymphocytes, and, occasionally, leukocytes can be found in some of the tissues. Some tissues have specialized cells that are not found in the others. The **matrix** in connective tissues gives the tissue its density. When a connective tissue has a high concentration of cells or fibers, it has proportionally a less dense matrix.

The organic portion or protein fibers found in connective tissues are either collagen, elastic, or reticular fibers. Collagen fibers provide strength to

the tissue, preventing it from being torn or separated from the surrounding tissues. Elastic fibers are made of the protein elastin; this fiber can stretch to one and one half of its length and return to its original size and shape. Elastic fibers provide flexibility to the tissues. Reticular fibers are the third type of protein fiber found in connective tissues. This fiber consists of thin strands of collagen that form a network of fibers to support the tissue and other organs to which it is connected. The various types of connective tissues, the types of cells and fibers they are made of, and sample locations of the tissues is summarized in [\[link\]](#).

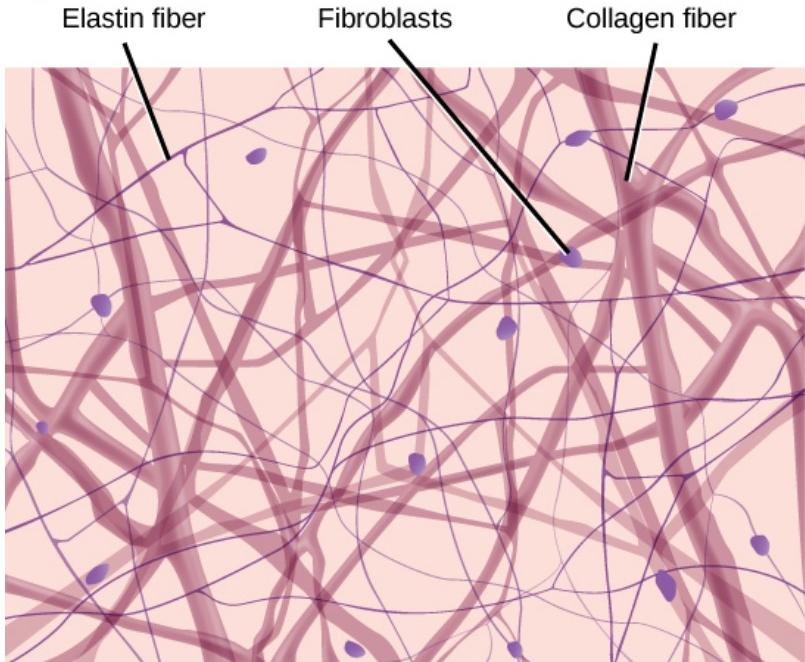
Connective Tissues			
Tissue	Cells	Fibers	Location
loose/ areolar	fibroblasts, macrophages some lymphocytes, some neutrophils	few: collagen, elastic, reticular	around blood vessels; anchors epithelia
dense, fibrous connective tissue	fibroblasts, macrophages	mostly collagen	irregular: skin; regular: tendons, ligaments

cartilage	chondrocytes chondroblasts	hyaline: few collagen	shark skeleton, fibrocartilage fetal bones, large amount of collagen human ears, intervertebral discs
bone	osteoblasts, osteocytes, osteoclasts	some: collagen, elastic	vertebrate skeletons
adipose blood	adipocytes red blood cells, white blood cells	few none	adipose (fat) blood

Loose/Areolar Connective Tissue

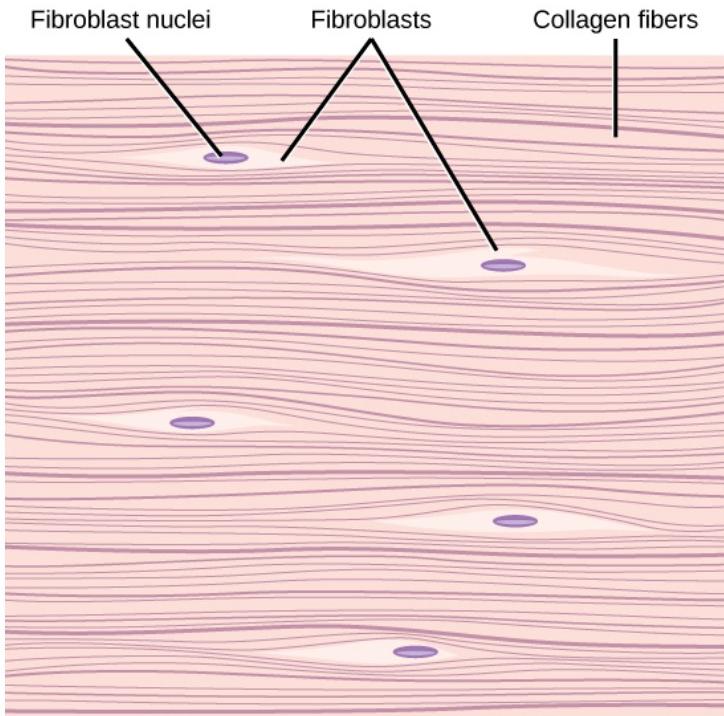
Loose connective tissue, also called areolar connective tissue, has a sampling of all of the components of a connective tissue. As illustrated in [\[link\]](#), loose connective tissue has some fibroblasts; macrophages are present as well. Collagen fibers are relatively wide and stain a light pink, while elastic fibers are thin and stain dark blue to black. The space between the formed elements of the tissue is filled with the matrix. The material in the connective tissue gives it a loose consistency similar to a cotton ball that has been pulled apart. Loose connective tissue is found around every blood vessel and helps to keep the vessel in place. The tissue is also found around and between most body organs. In summary, areolar tissue is tough, yet flexible, and

comprises membranes.



Fibrous Connective Tissue

Fibrous connective tissues contain large amounts of collagen fibers and few cells or matrix material. The fibers can be arranged irregularly or regularly with the strands lined up in parallel. Irregularly arranged fibrous connective tissues are found in areas of the body where stress occurs from all directions, such as the dermis of the skin. Regular fibrous connective tissue, shown in [\[link\]](#), is found in tendons (which connect muscles to bones) and ligaments (which connect bones to bones).

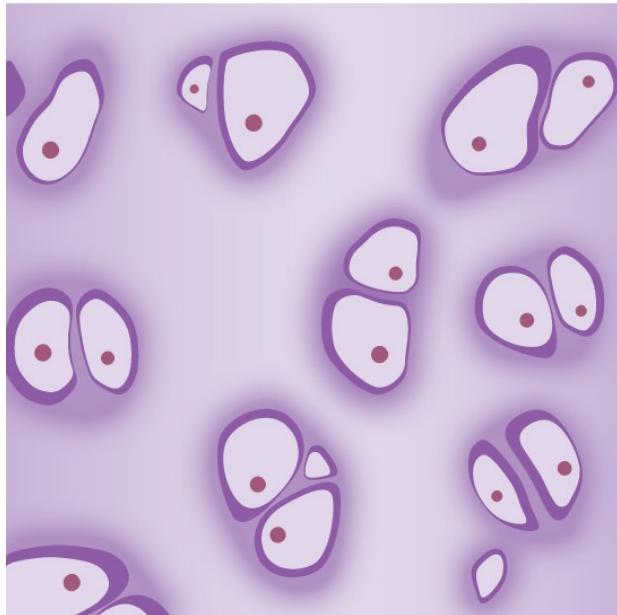


Cartilage

Cartilage is a connective tissue with a large amount of the matrix and variable amounts of fibers. The cells, called **chondrocytes**, make the matrix and fibers of the tissue. Chondrocytes are found in spaces within the tissue called **lacunae**.

A cartilage with few collagen and elastic fibers is hyaline cartilage, illustrated in [\[link\]](#). The lacunae are randomly scattered throughout the tissue and the matrix takes on a milky or scrubbed appearance with routine histological stains. Sharks have cartilaginous skeletons, as does nearly the entire

human skeleton during a specific pre-birth developmental stage. A remnant of this cartilage persists in the outer portion of the human nose. Hyaline cartilage is also found at the ends of long bones, reducing friction and cushioning the articulations of these bones.



Elastic cartilage has a large amount of elastic fibers, giving it tremendous flexibility. The ears of most vertebrate animals contain this cartilage as do portions of the larynx, or voice box. Fibrocartilage contains a large amount of collagen fibers, giving the tissue tremendous strength. Fibrocartilage comprises the intervertebral discs in vertebrate animals. Hyaline cartilage found in movable joints such as the knee and shoulder becomes damaged as a result of age or trauma. Damaged hyaline cartilage is replaced by fibrocartilage and results in the joints

becoming “stiff.”

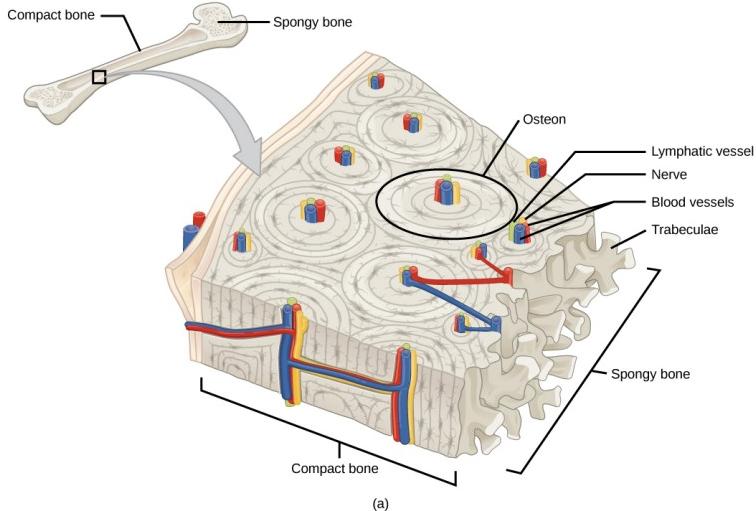
Bone

Bone, or osseous tissue, is a connective tissue that has a large amount of two different types of matrix material. The organic matrix is similar to the matrix material found in other connective tissues, including some amount of collagen and elastic fibers. This gives strength and flexibility to the tissue. The inorganic matrix consists of mineral salts—mostly calcium salts—that give the tissue hardness. Without adequate organic material in the matrix, the tissue breaks; without adequate inorganic material in the matrix, the tissue bends.

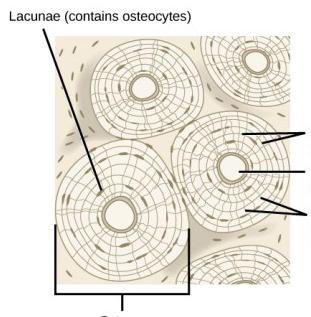
There are three types of cells in bone: osteoblasts, osteocytes, and osteoclasts. Osteoblasts are active in making bone for growth and remodeling. Osteoblasts deposit bone material into the matrix and, after the matrix surrounds them, they continue to live, but in a reduced metabolic state as osteocytes. Osteocytes are found in lacunae of the bone. Osteoclasts are active in breaking down bone for bone remodeling, and they provide access to calcium stored in tissues. Osteoclasts are usually found on the surface of the tissue.

Bone can be divided into two types: compact and spongy. Compact bone is found in the shaft (or diaphysis) of a long bone and the surface of the flat

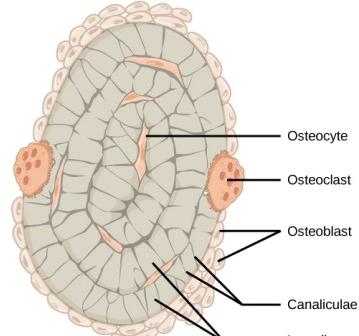
bones, while spongy bone is found in the end (or epiphysis) of a long bone. Compact bone is organized into subunits called **osteons**, as illustrated in [\[link\]](#). A blood vessel and a nerve are found in the center of the structure within the Haversian canal, with radiating circles of lacunae around it known as lamellae. The wavy lines seen between the lacunae are microchannels called **canalliculi**; they connect the lacunae to aid diffusion between the cells. Spongy bone is made of tiny plates called **trabeculae**; these plates serve as struts to give the spongy bone strength. Over time, these plates can break causing the bone to become less resilient. Bone tissue forms the internal skeleton of vertebrate animals, providing structure to the animal and points of attachment for tendons.



(a)



(b)

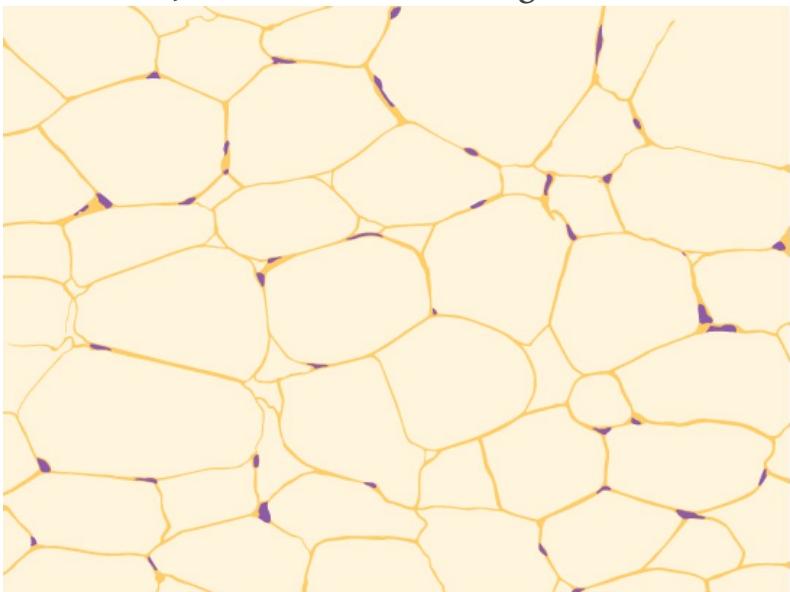


(c)

Adipose Tissue

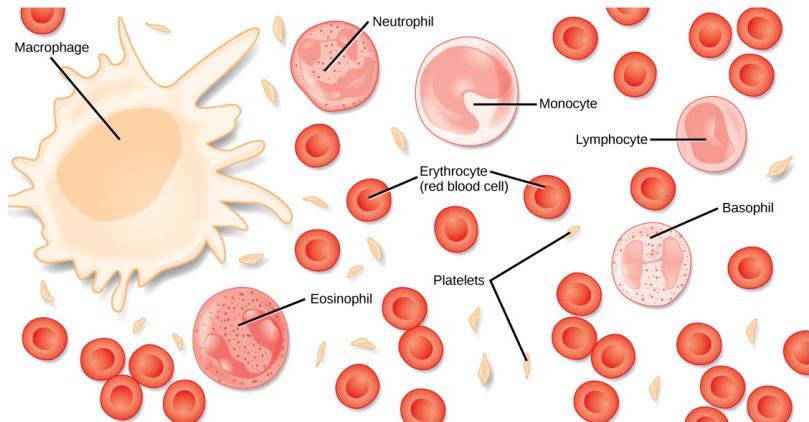
Adipose tissue, or fat tissue, is considered a connective tissue even though it does not have fibroblasts or a real matrix and only has a few fibers. Adipose tissue is made up of cells called adipocytes that collect and store fat in the form of triglycerides, for energy metabolism. Adipose tissues additionally serve as insulation to help maintain body temperatures, allowing animals to be

endothermic, and they function as cushioning against damage to body organs. Under a microscope, adipose tissue cells appear empty due to the extraction of fat during the processing of the material for viewing, as seen in [\[link\]](#). The thin lines in the image are the cell membranes, and the nuclei are the small, black dots at the edges of the cells.



Blood

Blood is considered a connective tissue because it has a matrix, as shown in [\[link\]](#). The living cell types are red blood cells (RBC), also called erythrocytes, and white blood cells (WBC), also called leukocytes. The fluid portion of whole blood, its matrix, is commonly called plasma.



The cell found in greatest abundance in blood is the erythrocyte. Erythrocytes are counted in millions in a blood sample: the average number of red blood cells in primates is 4.7 to 5.5 million cells per microliter. Erythrocytes are consistently the same size in a species, but vary in size between species. For example, the average diameter of a primate red blood cell is 7.5 μl , a dog is close at 7.0 μl , but a cat's RBC diameter is 5.9 μl . Sheep erythrocytes are even smaller at 4.6 μl . Mammalian erythrocytes lose their nuclei and mitochondria when they are released from the bone marrow where they are made. Fish, amphibian, and avian red blood cells maintain their nuclei and mitochondria throughout the cell's life. The principal job of an erythrocyte is to carry and deliver oxygen to the tissues.

Leukocytes are the predominant white blood cells found in the peripheral blood. Leukocytes are counted in the thousands in the blood with measurements expressed as ranges: primate counts

range from 4,800 to 10,800 cells per μl , dogs from 5,600 to 19,200 cells per μl , cats from 8,000 to 25,000 cells per μl , cattle from 4,000 to 12,000 cells per μl , and pigs from 11,000 to 22,000 cells per μl .

Lymphocytes function primarily in the immune response to foreign antigens or material. Different types of lymphocytes make antibodies tailored to the foreign antigens and control the production of those antibodies. Neutrophils are phagocytic cells and they participate in one of the early lines of defense against microbial invaders, aiding in the removal of bacteria that has entered the body. Another leukocyte that is found in the peripheral blood is the monocyte. Monocytes give rise to phagocytic macrophages that clean up dead and damaged cells in the body, whether they are foreign or from the host animal. Two additional leukocytes in the blood are eosinophils and basophils—both help to facilitate the inflammatory response.

The slightly granular material among the cells is a cytoplasmic fragment of a cell in the bone marrow. This is called a platelet or thrombocyte. Platelets participate in the stages leading up to coagulation of the blood to stop bleeding through damaged blood vessels. Blood has a number of functions, but primarily it transports material through the body to bring nutrients to cells and remove waste material from them.

Smooth muscle cells do not have striations, while

skeletal muscle cells do. Cardiac muscle cells have striations, but, unlike the multinucleate skeletal cells, they have only one nucleus. Cardiac muscle tissue also has intercalated discs, specialized regions running along the plasma membrane that join adjacent cardiac muscle cells and assist in passing an electrical impulse from cell to cell.

Muscle Tissues

There are three types of muscle in animal bodies: smooth, skeletal, and cardiac. They differ by the presence or absence of striations or bands, the number and location of nuclei, whether they are voluntarily or involuntarily controlled, and their location within the body. [\[link\]](#) summarizes these differences.

Type of Muscle	Striations	Nuclei	Control	Location
smooth	no	single, in center	involuntary	visceral organs
skeletal	yes	many, at periphery	voluntary	skeletal muscles

cardiac

yes

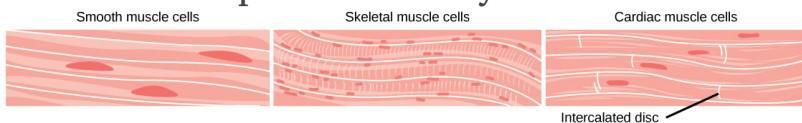
single, in heart center

involuntary

Smooth Muscle

Smooth muscle does not have striations in its cells. It has a single, centrally located nucleus, as shown in [\[link\]](#). Constriction of smooth muscle occurs under involuntary, autonomic nervous control and in response to local conditions in the tissues.

Smooth muscle tissue is also called non-striated as it lacks the banded appearance of skeletal and cardiac muscle. The walls of blood vessels, the tubes of the digestive system, and the tubes of the reproductive systems are composed of mostly smooth muscle.



Skeletal Muscle

Skeletal muscle has striations across its cells caused by the arrangement of the contractile proteins actin and myosin. These muscle cells are relatively long and have multiple nuclei along the edge of the cell. Skeletal muscle is under voluntary, somatic nervous system control and is found in the muscles that move bones. [\[link\]](#) illustrates the histology of skeletal muscle.

Cardiac Muscle

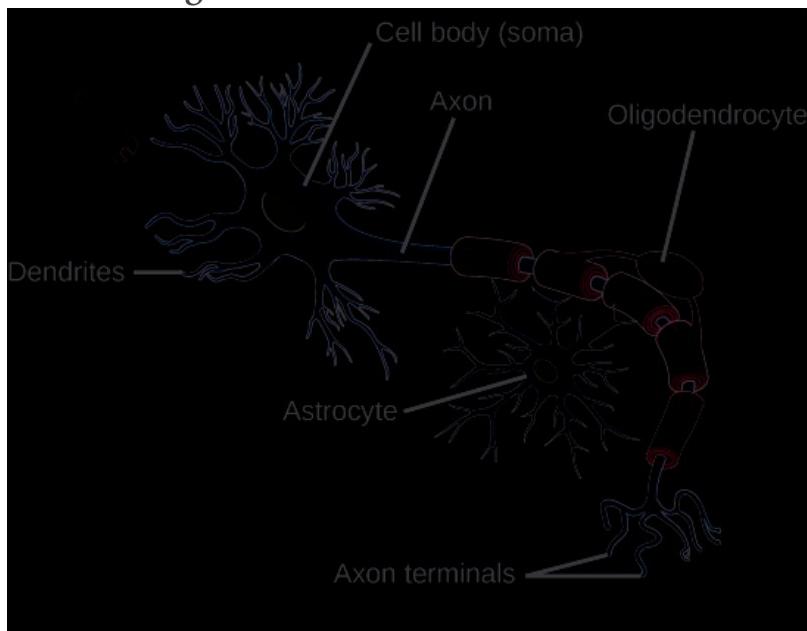
Cardiac muscle, shown in [\[link\]](#), is found only in the heart. Like skeletal muscle, it has cross striations in its cells, but cardiac muscle has a single, centrally located nucleus. Cardiac muscle is not under voluntary control but can be influenced by the autonomic nervous system to speed up or slow down. An added feature to cardiac muscle cells is a line that extends along the end of the cell as it abuts the next cardiac cell in the row. This line is called an intercalated disc: it assists in passing electrical impulse efficiently from one cell to the next and maintains the strong connection between neighboring cardiac cells.

The neuron has projections called dendrites that receive signals and projections called axons that send signals. Also shown are two types of glial cells: astrocytes regulate the chemical environment of the nerve cell, and oligodendrocytes insulate the axon so the electrical nerve impulse is transferred more efficiently.

Nervous Tissues

Nervous tissues are made of cells specialized to receive and transmit electrical impulses from specific areas of the body and to send them to specific locations in the body. The main cell of the nervous system is the neuron, illustrated in [\[link\]](#). The large structure with a central nucleus is the cell

body of the neuron. Projections from the cell body are either dendrites specialized in receiving input or a single axon specialized in transmitting impulses. Some glial cells are also shown. Astrocytes regulate the chemical environment of the nerve cell, and oligodendrocytes insulate the axon so the electrical nerve impulse is transferred more efficiently. Other glial cells that are not shown support the nutritional and waste requirements of the neuron. Some of the glial cells are phagocytic and remove debris or damaged cells from the tissue. A nerve consists of neurons and glial cells.



Link to Learning

Click through the [interactive review](#) to learn more

about epithelial tissues.

Career Connections

Pathologist

A pathologist is a medical doctor or veterinarian who has specialized in the laboratory detection of disease in animals, including humans. These professionals complete medical school education and follow it with an extensive post-graduate residency at a medical center. A pathologist may oversee clinical laboratories for the evaluation of body tissue and blood samples for the detection of disease or infection. They examine tissue specimens through a microscope to identify cancers and other diseases. Some pathologists perform autopsies to determine the cause of death and the progression of disease.

Section Summary

The basic building blocks of complex animals are four primary tissues. These are combined to form organs, which have a specific, specialized function within the body, such as the skin or kidney. Organs

are organized together to perform common functions in the form of systems. The four primary tissues are epithelia, connective tissues, muscle tissues, and nervous tissues.

Visual Connection Questions

[\[link\]](#) Which of the following statements about types of epithelial cells is false?

1. Simple columnar epithelial cells line the tissue of the lung.
2. Simple cuboidal epithelial cells are involved in the filtering of blood in the kidney.
3. Pseudostratified columnar epithilia occur in a single layer, but the arrangement of nuclei makes it appear that more than one layer is present.
4. Transitional epithelia change in thickness depending on how full the bladder is.

[\[link\]](#) A

Review Questions

Which type of epithelial cell is best adapted to aid diffusion?

1. squamous
 2. cuboidal
 3. columnar
 4. transitional
-

C

Which type of epithelial cell is found in glands?

1. squamous
 2. cuboidal
 3. columnar
 4. transitional
-

B

Which type of epithelial cell is found in the urinary bladder?

1. squamous
 2. cuboidal
 3. columnar
 4. transitional
-

D

Which type of connective tissue has the most fibers?

1. loose connective tissue
 2. fibrous connective tissue
 3. cartilage
 4. bone
-

B

Which type of connective tissue has a mineralized different matrix?

1. loose connective tissue
 2. fibrous connective tissue
 3. cartilage
 4. bone
-

D

The cell found in bone that breaks it down is called an ____.

1. osteoblast
2. osteocyte

3. osteoclast

4. osteon

C

The cell found in bone that makes the bone is called an _____.

1. osteoblast

2. osteocyte

3. osteoclast

4. osteon

A

Plasma is the _____.

1. fibers in blood

2. matrix of blood

3. cell that phagocytizes bacteria

4. cell fragment found in the tissue

B

The type of muscle cell under voluntary control is the _____.

-
1. smooth muscle
 2. skeletal muscle
 3. cardiac muscle
 4. visceral muscle

B

The part of a neuron that contains the nucleus is the

1. cell body
2. dendrite
3. axon
4. glial

A

Why are intercalated discs essential to the function of cardiac muscle?

1. The discs maintain the barriers between the cells.
2. The discs pass nutrients between cells.
3. The discs ensure that all the cardiac muscle cells beat as a single unit.
4. The discs control the heart rate.

Critical Thinking Questions

How can squamous epithelia both facilitate diffusion and prevent damage from abrasion?

Squamous epithelia can be either simple or stratified. As a single layer of cells, it presents a very thin epithelia that minimally inhibits diffusion. As a stratified epithelia, the surface cells can be sloughed off and the cells in deeper layers protect the underlying tissues from damage.

What are the similarities between cartilage and bone?

Both contain cells other than the traditional fibroblast. Both have cells that lodge in spaces within the tissue called lacunae. Both collagen and elastic fibers are found in bone and cartilage. Both tissues participate in vertebrate skeletal development and formation.

Multiple sclerosis is a debilitating autoimmune disease that results in the loss of the insulation around neuron axons. What cell type is the immune system attacking, and how does this disrupt the transfer of messages by the nervous system?

In multiple sclerosis, the immune system attacks the oligodendrocytes. The death of oligodendrocytes results in the loss of the insulating sheath around the axon of the neurons. When the sheath is gone, the electrical impulses travel much more slowly down the length of the axon.

When a person leads a sedentary life his skeletal muscles atrophy, but his smooth muscles do not. Why?

Skeletal muscles are involved in voluntary motion, so the person has to make the choice to work those muscles through exercise or movement. Smooth muscles are involved in involuntary activities of the body (ex. blood vessel expansion and contraction, intestinal peristalsis) so they are active even when a person is sedentary.

Glossary

canaliculus

microchannel that connects the lacunae and aids diffusion between cells

cartilage

type of connective tissue with a large amount of ground substance matrix, cells called chondrocytes, and some amount of fibers

chondrocyte

cell found in cartilage

columnar epithelia

epithelia made of cells taller than they are wide, specialized in absorption

connective tissue

type of tissue made of cells, ground substance matrix, and fibers

cuboidal epithelia

epithelia made of cube-shaped cells, specialized in glandular functions

epithelial tissue

tissue that either lines or covers organs or other tissues

fibrous connective tissue

type of connective tissue with a high

concentration of fibers

lacuna

space in cartilage and bone that contains living cells

loose (areolar) connective tissue

type of connective tissue with small amounts of cells, matrix, and fibers; found around blood vessels

matrix

component of connective tissue made of both living and nonliving (ground substances) cells

osteon

subunit of compact bone

pseudostratified

layer of epithelia that appears multilayered, but is a simple covering

simple epithelia

single layer of epithelial cells

squamous epithelia

type of epithelia made of flat cells, specialized in aiding diffusion or preventing abrasion

stratified epithelia

multiple layers of epithelial cells

trabecula

tiny plate that makes up spongy bone and gives it strength

transitional epithelia

epithelia that can transition from appearing multilayered to simple; also called uroepithelial

Homeostasis

By the end of this section, you will be able to:

- Define homeostasis
- Describe the factors affecting homeostasis
- Discuss positive and negative feedback mechanisms used in homeostasis
- Describe thermoregulation of endothermic and ectothermic animals

Animal organs and organ systems constantly adjust to internal and external changes through a process called homeostasis (“steady state”). These changes might be in the level of glucose or calcium in blood or in external temperatures. **Homeostasis** means to maintain dynamic equilibrium in the body. It is dynamic because it is constantly adjusting to the changes that the body’s systems encounter. It is equilibrium because body functions are kept within specific ranges. Even an animal that is apparently inactive is maintaining this homeostatic equilibrium.

Homeostatic Process

The goal of homeostasis is the maintenance of equilibrium around a point or value called a **set point**. While there are normal fluctuations from the set point, the body’s systems will usually attempt to

go back to this point. A change in the internal or external environment is called a stimulus and is detected by a receptor; the response of the system is to adjust the deviation parameter toward the set point. For instance, if the body becomes too warm, adjustments are made to cool the animal. If the blood's glucose rises after a meal, adjustments are made to lower the blood glucose level by getting the nutrient into tissues that need it or to store it for later use.

Blood sugar levels are controlled by a negative feedback loop. (credit: modification of work by Jon Sullivan)

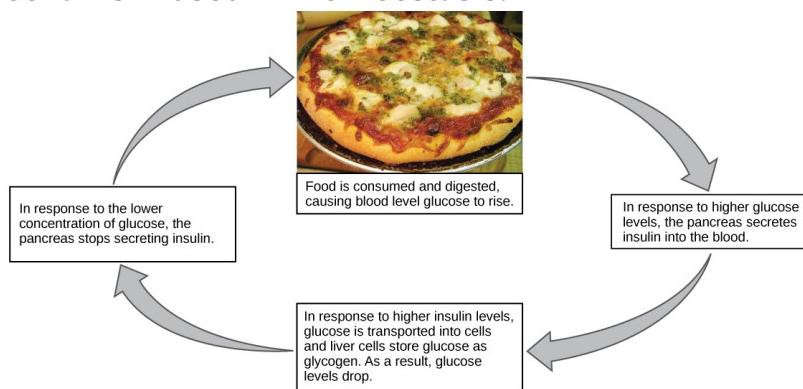
Control of Homeostasis

When a change occurs in an animal's environment, an adjustment must be made. The receptor senses the change in the environment, then sends a signal to the control center (in most cases, the brain) which in turn generates a response that is signaled to an effector. The effector is a muscle (that contracts or relaxes) or a gland that secretes. Homeostasis is maintained by negative feedback loops. Positive feedback loops actually push the organism further out of homeostasis, but may be necessary for life to occur. Homeostasis is controlled by the nervous and endocrine system of mammals.

Negative Feedback Mechanisms

Any homeostatic process that changes the direction of the stimulus is a **negative feedback loop**. It may either increase or decrease the stimulus, but the stimulus is not allowed to continue as it did before the receptor sensed it. In other words, if a level is too high, the body does something to bring it down, and conversely, if a level is too low, the body does something to make it go up. Hence the term negative feedback. An example is animal maintenance of blood glucose levels. When an animal has eaten, blood glucose levels rise. This is sensed by the nervous system. Specialized cells in the pancreas sense this, and the hormone insulin is released by the endocrine system. Insulin causes blood glucose levels to decrease, as would be expected in a negative feedback system, as illustrated in [\[link\]](#). However, if an animal has not eaten and blood glucose levels decrease, this is sensed in another group of cells in the pancreas, and the hormone glucagon is released causing glucose levels to increase. This is still a negative feedback loop, but not in the direction expected by the use of the term “negative.” Another example of an increase as a result of the feedback loop is the control of blood calcium. If calcium levels decrease, specialized cells in the parathyroid gland sense this and release parathyroid hormone (PTH), causing an increased absorption of calcium through the intestines and kidneys and, possibly, the breakdown of bone in order to liberate calcium. The effects of PTH are to raise blood levels of the element.

Negative feedback loops are the predominant mechanism used in homeostasis.



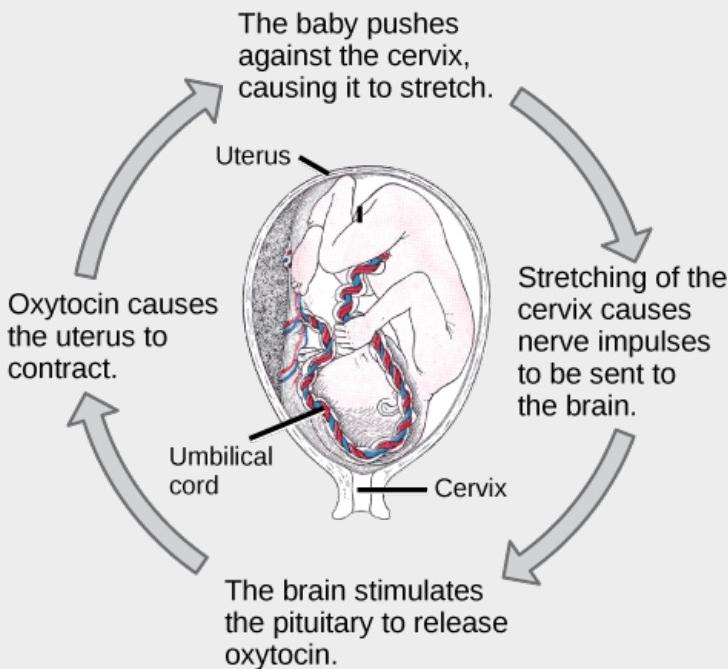
Positive Feedback Loop

A **positive feedback loop** maintains the direction of the stimulus, possibly accelerating it. Few examples of positive feedback loops exist in animal bodies, but one is found in the cascade of chemical reactions that result in blood clotting, or coagulation. As one clotting factor is activated, it activates the next factor in sequence until a fibrin clot is achieved. The direction is maintained, not changed, so this is positive feedback. Another example of positive feedback is uterine contractions during childbirth, as illustrated in [\[link\]](#). The hormone oxytocin, made by the endocrine system, stimulates the contraction of the uterus. This produces pain sensed by the nervous system. Instead of lowering the oxytocin and causing the pain to subside, more oxytocin is produced until the contractions are powerful enough to produce

childbirth.

Art Connection

The birth of a human infant is the result of positive feedback.



State whether each of the following processes is regulated by a positive feedback loop or a negative feedback loop.

1. A person feels satiated after eating a large meal.
2. The blood has plenty of red blood cells. As a result, erythropoietin, a hormone that stimulates the production of new red blood

cells, is no longer released from the kidney.

Set Point

It is possible to adjust a system's set point. When this happens, the feedback loop works to maintain the new setting. An example of this is blood pressure: over time, the normal or set point for blood pressure can increase as a result of continued increases in blood pressure. The body no longer recognizes the elevation as abnormal and no attempt is made to return to the lower set point. The result is the maintenance of an elevated blood pressure that can have harmful effects on the body. Medication can lower blood pressure and lower the set point in the system to a more healthy level. This is called a process of **alteration** of the set point in a feedback loop.

Changes can be made in a group of body organ systems in order to maintain a set point in another system. This is called **acclimatization**. This occurs, for instance, when an animal migrates to a higher altitude than it is accustomed to. In order to adjust to the lower oxygen levels at the new altitude, the body increases the number of red blood cells circulating in the blood to ensure adequate oxygen delivery to the tissues. Another example of acclimatization is animals that have seasonal

changes in their coats: a heavier coat in the winter ensures adequate heat retention, and a light coat in summer assists in keeping body temperature from rising to harmful levels.

Link to Learning



Feedback mechanisms can be understood in terms of driving a race car along a track: watch a short video lesson on positive and negative feedback loops.

https://www.openstaxcollege.org/l/feedback_loops

Homeostasis: Thermoregulation

Body temperature affects body activities. Generally, as body temperature rises, enzyme activity rises as well. For every ten degree centigrade rise in

temperature, enzyme activity doubles, up to a point. Body proteins, including enzymes, begin to denature and lose their function with high heat (around 50°C for mammals). Enzyme activity will decrease by half for every ten degree centigrade drop in temperature, to the point of freezing, with a few exceptions. Some fish can withstand freezing solid and return to normal with thawing.

Link to Learning



Watch this Discovery Channel video on thermoregulation to see illustrations of this process in a variety of animals.

<https://www.openstaxcollege.org/l/thermoregulate>

Heat can be exchanged by four mechanisms: (a) radiation, (b) evaporation, (c) convection, or (d) conduction. (credit b: modification of work by “Kullez”/Flickr; credit c: modification of work by

Chad Rosenthal; credit d: modification of work by
“stacey.d”/Flickr)

Endotherms and Ectotherms

Animals can be divided into two groups: some maintain a constant body temperature in the face of differing environmental temperatures, while others have a body temperature that is the same as their environment and thus varies with the environment. Animals that do not control their body temperature are ectotherms. This group has been called cold-blooded, but the term may not apply to an animal in the desert with a very warm body temperature. In contrast to ectotherms, which rely on external temperatures to set their body temperatures, poikilotherms are animals with constantly varying internal temperatures. An animal that maintains a constant body temperature in the face of environmental changes is called a homeotherm. Endotherms are animals that rely on internal sources for body temperature but which can exhibit extremes in temperature. These animals are able to maintain a level of activity at cooler temperature, which an ectotherm cannot due to differing enzyme levels of activity.

Heat can be exchanged between an animal and its environment through four mechanisms: radiation, evaporation, convection, and conduction ([\[link\]](#)). Radiation is the emission of electromagnetic “heat”

waves. Heat comes from the sun in this manner and radiates from dry skin the same way. Heat can be removed with liquid from a surface during evaporation. This occurs when a mammal sweats. Convection currents of air remove heat from the surface of dry skin as the air passes over it. Heat will be conducted from one surface to another during direct contact with the surfaces, such as an animal resting on a warm rock.



(a) Radiation

(b) Evaporation



(c) Convection

(d) Conduction

Heat Conservation and Dissipation

Animals conserve or dissipate heat in a variety of ways. In certain climates, endothermic animals have some form of insulation, such as fur, fat, feathers, or some combination thereof. Animals with thick fur or

feathers create an insulating layer of air between their skin and internal organs. Polar bears and seals live and swim in a subfreezing environment and yet maintain a constant, warm, body temperature. The arctic fox, for example, uses its fluffy tail as extra insulation when it curls up to sleep in cold weather. Mammals have a residual effect from shivering and increased muscle activity: arrector pili muscles cause “goose bumps,” causing small hairs to stand up when the individual is cold; this has the intended effect of increasing body temperature. Mammals use layers of fat to achieve the same end. Loss of significant amounts of body fat will compromise an individual’s ability to conserve heat.

Endotherms use their circulatory systems to help maintain body temperature. Vasodilation brings more blood and heat to the body surface, facilitating radiation and evaporative heat loss, which helps to cool the body. Vasoconstriction reduces blood flow in peripheral blood vessels, forcing blood toward the core and the vital organs found there, and conserving heat. Some animals have adaptions to their circulatory system that enable them to transfer heat from arteries to veins, warming blood returning to the heart. This is called a countercurrent heat exchange; it prevents the cold venous blood from cooling the heart and other internal organs. This adaption can be shut down in some animals to prevent overheating the internal organs. The countercurrent adaption is found in many animals,

including dolphins, sharks, bony fish, bees, and hummingbirds. In contrast, similar adaptations can help cool endotherms when needed, such as dolphin flukes and elephant ears.

Some ectothermic animals use changes in their behavior to help regulate body temperature. For example, a desert ectothermic animal may simply seek cooler areas during the hottest part of the day in the desert to keep from getting too warm. The same animals may climb onto rocks to capture heat during a cold desert night. Some animals seek water to aid evaporation in cooling them, as seen with reptiles. Other ectotherms use group activity such as the activity of bees to warm a hive to survive winter.

Many animals, especially mammals, use metabolic waste heat as a heat source. When muscles are contracted, most of the energy from the ATP used in muscle actions is wasted energy that translates into heat. Severe cold elicits a shivering reflex that generates heat for the body. Many species also have a type of adipose tissue called brown fat that specializes in generating heat.

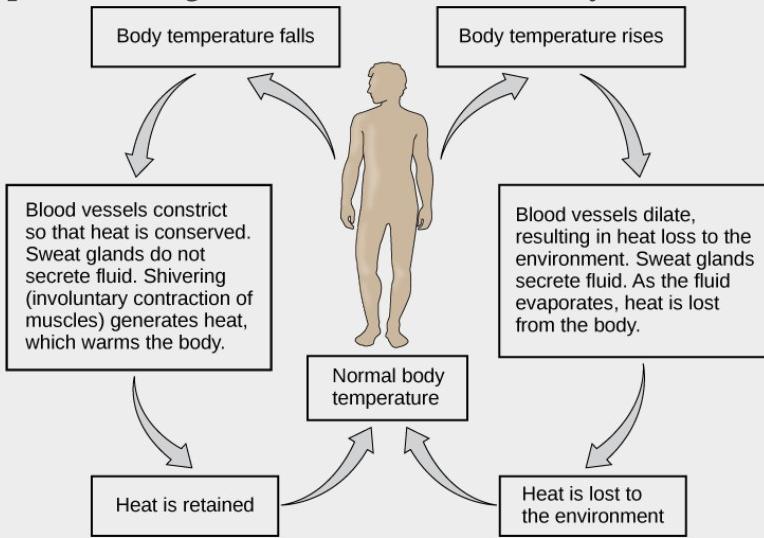
Neural Control of Thermoregulation

The nervous system is important to thermoregulation, as illustrated in [\[link\]](#). The

processes of homeostasis and temperature control are centered in the hypothalamus of the advanced animal brain.

Art Connection

The body is able to regulate temperature in response to signals from the nervous system.



When bacteria are destroyed by leukocytes, pyrogens are released into the blood. Pyrogens reset the body's thermostat to a higher temperature, resulting in fever. How might pyrogens cause the body temperature to rise?

The hypothalamus maintains the set point for body temperature through reflexes that cause vasodilation

and sweating when the body is too warm, or vasoconstriction and shivering when the body is too cold. It responds to chemicals from the body. When a bacterium is destroyed by phagocytic leukocytes, chemicals called endogenous pyrogens are released into the blood. These pyrogens circulate to the hypothalamus and reset the thermostat. This allows the body's temperature to increase in what is commonly called a fever. An increase in body temperature causes iron to be conserved, which reduces a nutrient needed by bacteria. An increase in body heat also increases the activity of the animal's enzymes and protective cells while inhibiting the enzymes and activity of the invading microorganisms. Finally, heat itself may also kill the pathogen. A fever that was once thought to be a complication of an infection is now understood to be a normal defense mechanism.

Section Summary

Homeostasis is a dynamic equilibrium that is maintained in body tissues and organs. It is dynamic because it is constantly adjusting to the changes that the systems encounter. It is in equilibrium because body functions are kept within a normal range, with some fluctuations around a set point for the processes.

Art Connections

[\[link\]](#) State whether each of the following processes are regulated by a positive feedback loop or a negative feedback loop.

1. A person feels satiated after eating a large meal.
2. The blood has plenty of red blood cells. As a result, erythropoietin, a hormone that stimulates the production of new red blood cells, is no longer released from the kidney.

[\[link\]](#) Both processes are the result of negative feedback loops. Negative feedback loops, which tend to keep a system at equilibrium, are more common than positive feedback loops.

[\[link\]](#) When bacteria are destroyed by leuckocytes, pyrogens are released into the blood. Pyrogens reset the body's thermostat to a higher temperature, resulting in fever. How might pyrogens cause the body temperature to rise?

[\[link\]](#) Pyrogens increase body temperature by

causing the blood vessels to constrict, inducing shivering, and stopping sweat glands from secreting fluid.

Review Questions

When faced with a sudden drop in environmental temperature, an endothermic animal will:

1. experience a drop in its body temperature
2. wait to see if it goes lower
3. increase muscle activity to generate heat
4. add fur or fat to increase insulation

C

Which is an example of negative feedback?

1. lowering of blood glucose after a meal
2. blood clotting after an injury
3. lactation during nursing
4. uterine contractions during labor

A

Which method of heat exchange occurs during direct contact between the source and animal?

1. radiation
 2. evaporation
 3. convection
 4. conduction
-

D

The body's thermostat is located in the _____.

1. homeostatic receptor
 2. hypothalamus
 3. medulla
 4. vasodilation center
-

B

Free Response

Why are negative feedback loops used to control body homeostasis?

An adjustment to a change in the internal or

external environment requires a change in the direction of the stimulus. A negative feedback loop accomplishes this, while a positive feedback loop would continue the stimulus and result in harm to the animal.

Why is a fever a “good thing” during a bacterial infection?

Mammalian enzymes increase activity to the point of denaturation, increasing the chemical activity of the cells involved. Bacterial enzymes have a specific temperature for their most efficient activity and are inhibited at either higher or lower temperatures. Fever results in an increase in the destruction of the invading bacteria by increasing the effectiveness of body defenses and an inhibiting bacterial metabolism.

How is a condition such as diabetes a good example of the failure of a set point in humans?

Diabetes is often associated with a lack in production of insulin. Without insulin, blood glucose levels go up after a meal, but never go back down to normal levels.

Glossary

acclimatization

alteration in a body system in response to environmental change

alteration

change of the set point in a homeostatic system

homeostasis

dynamic equilibrium maintaining appropriate body functions

negative feedback loop

feedback to a control mechanism that increases or decreases a stimulus instead of maintaining it

positive feedback loop

feedback to a control mechanism that continues the direction of a stimulus

set point

midpoint or target point in homeostasis

thermoregulation

regulation of body temperature

Nervous System

By the end of this section, you will be able to:

- Describe the form and function of a neuron
- Describe the basic parts and functions of the central nervous system
- Describe the basic parts and functions of the peripheral nervous system

As you read this, your nervous system is performing several functions simultaneously. The visual system is processing what is seen on the page; the motor system controls your eye movements and the turn of the pages (or click of the mouse); the prefrontal cortex maintains attention. Even fundamental functions, like breathing and regulation of body temperature, are controlled by the nervous system. The nervous system is one of two systems that exert control over all the organ systems of the body; the other is the endocrine system. The nervous system's control is much more specific and rapid than the hormonal system. It communicates signals through cells and the tiny gaps between them rather than through the circulatory system as in the endocrine system. It uses a combination of chemical and electrochemical signals, rather than purely chemical signals used by the endocrine system to cover long distances quickly. The nervous system acquires information from sensory organs, processes it and then may initiate a response either through motor function, leading to movement, or in a change in the

organism's physiological state.

Nervous systems throughout the animal kingdom vary in structure and complexity. Some organisms, like sea sponges, lack a true nervous system. Others, like jellyfish, lack a true brain and instead have a system of separate but connected nerve cells (neurons) called a “nerve net.” Flatworms have both a central nervous system (CNS), made up of a ganglion (clusters of connected neurons) and two nerve cords, and a peripheral nervous system (PNS) containing a system of nerves that extend throughout the body. The insect nervous system is more complex but also fairly decentralized. It contains a brain, ventral nerve cord, and ganglia. These ganglia can control movements and behaviors without input from the brain.

Compared to invertebrates, vertebrate nervous systems are more complex, centralized, and specialized. While there is great diversity among different vertebrate nervous systems, they all share a basic structure: a CNS that contains a brain and spinal cord and a PNS made up of peripheral sensory and motor nerves. One interesting difference between the nervous systems of invertebrates and vertebrates is that the nerve cords of many invertebrates are located ventrally (toward the stomach) whereas the vertebrate spinal cords are located dorsally (toward the back). There is debate among evolutionary biologists as to whether

these different nervous system plans evolved separately or whether the invertebrate body plan arrangement somehow “flipped” during the evolution of vertebrates.

The nervous system is made up of **neurons**, specialized cells that can receive and transmit chemical or electrical signals, and **glia**, cells that provide support functions for the neurons. There is great diversity in the types of neurons and glia that are present in different parts of the nervous system. Neurons contain organelles common to other cells, such as a nucleus and mitochondria. They also have more specialized structures, including dendrites and axons.

Neurons and Glial Cells

The nervous system of the common laboratory fly, *Drosophila melanogaster*, contains around 100,000 neurons, the same number as a lobster. This number compares to 75 million in the mouse and 300 million in the octopus. A human brain contains around 86 billion neurons. Despite these very different numbers, the nervous systems of these animals control many of the same behaviors—from basic reflexes to more complicated behaviors like finding food and courting mates. The ability of neurons to communicate with each other as well as with other types of cells underlies all of these behaviors.

Most neurons share the same cellular components. But neurons are also highly specialized—different types of neurons have different sizes and shapes that relate to their functional roles.

Like other cells, each neuron has a cell body (or soma) that contains a nucleus, smooth and rough endoplasmic reticulum, Golgi apparatus, mitochondria, and other cellular components.

Neurons also contain unique structures for receiving and sending the electrical signals that make communication between neurons possible ([\[link\]](#)).

Dendrites are tree-like structures that extend away from the cell body to receive messages from other neurons at specialized junctions called **synapses**. Although some neurons do not have any dendrites, most have one or many dendrites.

The bilayer lipid membrane that surrounds a neuron is impermeable to ions. To enter or exit the neuron, ions must pass through ion channels that span the membrane. Some ion channels need to be activated to open and allow ions to pass into or out of the cell. These ion channels are sensitive to the environment and can change their shape accordingly. Ion channels that change their structure in response to voltage changes are called voltage-gated ion channels. The difference in total charge between the inside and outside of the cell is called the membrane potential.

A neuron at rest is negatively charged: the inside of a cell is approximately 70 millivolts more negative than the outside (-70 mV). This voltage is called the resting membrane potential; it is caused by differences in the concentrations of ions inside and outside the cell and the selective permeability created by ion channels. Sodium-potassium pumps in the membrane produce the different ion concentrations inside and outside of the cell by bringing in two K⁺ ions and removing three Na⁺ ions. The actions of this pump are costly: one molecule of ATP is used up for each turn. Up to 50 percent of a neuron's ATP is used in maintaining its membrane resting potential. Potassium ions (K⁺), which are higher inside the cell, move fairly freely out of the neuron through potassium channels; this loss of positive charge produces a net negative charge inside the cell. Sodium ions (Na⁺), which are low inside, have a driving force to enter but move less freely. Their channels are voltage dependent and will open when a slight change in the membrane potential triggers them.

A neuron can receive input from other neurons and, if this input is strong enough, send the signal to downstream neurons. Transmission of a signal between neurons is generally carried by a chemical, called a neurotransmitter, which diffuses from the axon of one neuron to the dendrite of a second neuron. When neurotransmitter molecules bind to receptors located on a neuron's dendrites, the

neurotransmitter opens ion channels in the dendrite's plasma membrane. This opening allows sodium ions to enter the neuron and results in **depolarization** of the membrane—a decrease in the voltage across the neuron membrane. Once a signal is received by the dendrite, it then travels passively to the cell body. A large enough signal from neurotransmitters will reach the axon. If it is strong enough (that is, if the **threshold of excitation**, a depolarization to around -60mV is reached), then depolarization creates a positive feedback loop: as more Na^+ ions enter the cell, the axon becomes further depolarized, opening even more sodium channels at further distances from the cell body. This will cause voltage dependent Na^+ channels further down the axon to open and more positive ions to enter the cell. In the axon, this “signal” will become a self-propagating brief reversal of the resting membrane potential called an **action potential**.

An action potential is an all-or-nothing event; it either happens or it does not. The threshold of excitation must be reached for the neuron to “fire” an action potential. As sodium ions rush into the cell, depolarization actually reverses the charge across the membrane from -70mV to $+30\text{mV}$. This change in the membrane potential causes voltage-gated K^+ channels to open, and K^+ begins to leave the cell, repolarizing it. At the same time, Na^+ channels inactivate so no more Na^+ enters the cell.

K^+ ions continue to leave the cell and the membrane potential returns to the resting potential. At the resting potential, the K^+ channels close and Na^+ channels reset. The depolarization of the membrane proceeds in a wave down the length of the axon. It travels in only one direction because the sodium channels have been inactivated and unavailable until the membrane potential is near the resting potential again; at this point they are reset to closed and can be opened again.

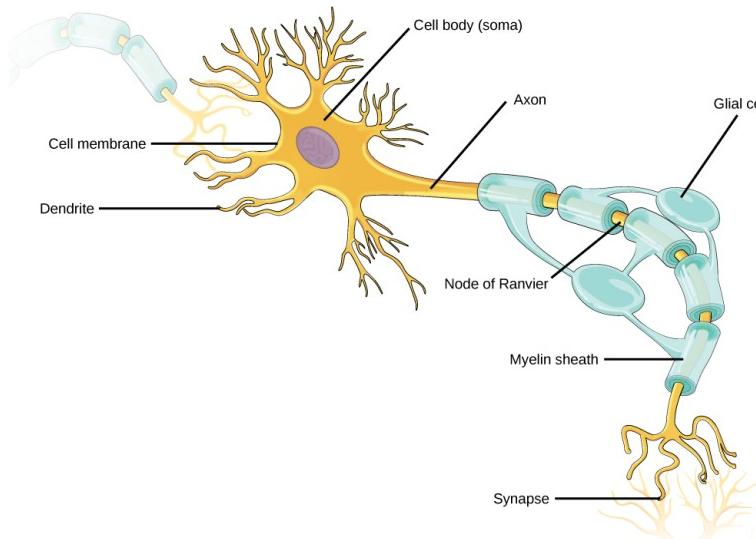
An **axon** is a tube-like structure that propagates the signal from the cell body to specialized endings called axon terminals. These terminals in turn then synapse with other neurons, muscle, or target organs. When the action potential reaches the axon terminal, this causes the release of neurotransmitter onto the dendrite of another neuron.

Neurotransmitters released at axon terminals allow signals to be communicated to these other cells, and the process begins again. Neurons usually have one or two axons, but some neurons do not contain any axons.

Some axons are covered with a special structure called a **myelin sheath**, which acts as an insulator to keep the electrical signal from dissipating as it travels down the axon. This insulation is important, as the axon from a human motor neuron can be as long as a meter (3.2 ft)—from the base of the spine to the toes. The myelin sheath is produced by glial

cells. Along the axon there are periodic gaps in the myelin sheath. These gaps are called nodes of Ranvier and are sites where the signal is “recharged” as it travels along the axon.

It is important to note that a single neuron does not act alone—neuronal communication depends on the connections that neurons make with one another (as well as with other cells, like muscle cells). Dendrites from a single neuron may receive synaptic contact from many other neurons. For example, dendrites from a Purkinje cell in the cerebellum are thought to receive contact from as many as 200,000 other neurons.

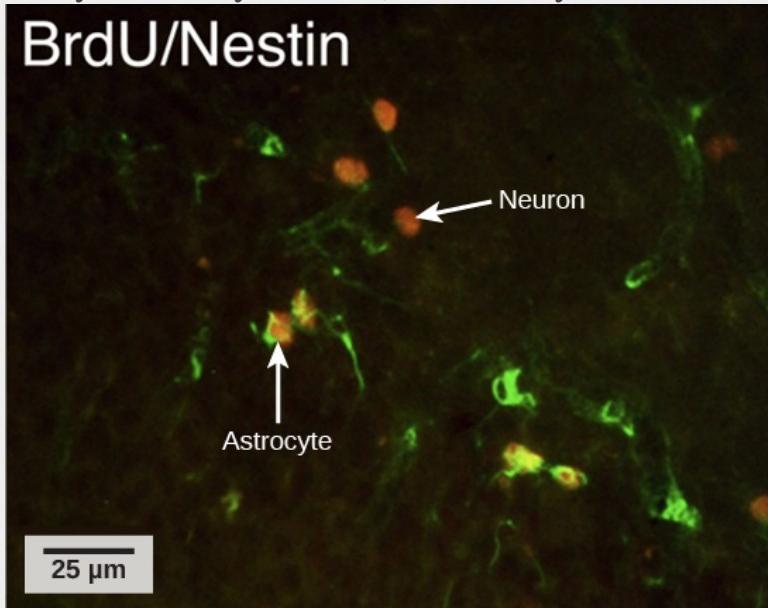


At one time, scientists believed that people were born with all the neurons they would ever have. Research performed during the last few decades indicates that neurogenesis, the birth of new neurons, continues into adulthood. Neurogenesis was first discovered in songbirds that produce new neurons while learning songs. For mammals, new neurons also play an important role in learning: about 1,000 new neurons develop in the hippocampus (a brain structure involved in learning and memory) each day. While most of the new neurons will die, researchers found that an increase in the number of surviving new neurons in the hippocampus correlated with how well rats learned a new task. Interestingly, both exercise and some antidepressant medications also promote neurogenesis in the hippocampus. Stress has the opposite effect. While neurogenesis is quite limited compared to regeneration in other tissues, research in this area may lead to new treatments for disorders such as Alzheimer's, stroke, and epilepsy.

How do scientists identify new neurons? A researcher can inject a compound called bromodeoxyuridine (BrdU) into the brain of an animal. While all cells will be exposed to BrdU, BrdU will only be incorporated into the DNA of newly generated cells that are in S phase. A technique called immunohistochemistry can be used to attach a fluorescent label to the incorporated BrdU, and a researcher can use fluorescent microscopy to visualize the presence of

BrdU, and thus new neurons, in brain tissue ([\[link\]](#)).

This image shows new neurons in a rat hippocampus. New neurons tagged with BrdU glow red in this micrograph. (credit: modification of work by Dr. Maryam Faiz, University of Barcelona)



Concept in Action

Visit this link [interactive lab](#) to see more information about neurogenesis, including an interactive laboratory simulation and a video that explains how BrdU labels new cells.

While glial cells are often thought of as the supporting cast of the nervous system, the number of glial cells in the brain actually outnumbers the number of neurons by a factor of 10. Neurons would be unable to function without the vital roles that are fulfilled by these glial cells. Glia guide developing neurons to their destinations, buffer ions and chemicals that would otherwise harm neurons, and provide myelin sheaths around axons. When glia do not function properly, the result can be disastrous—most brain tumors are caused by mutations in glia.

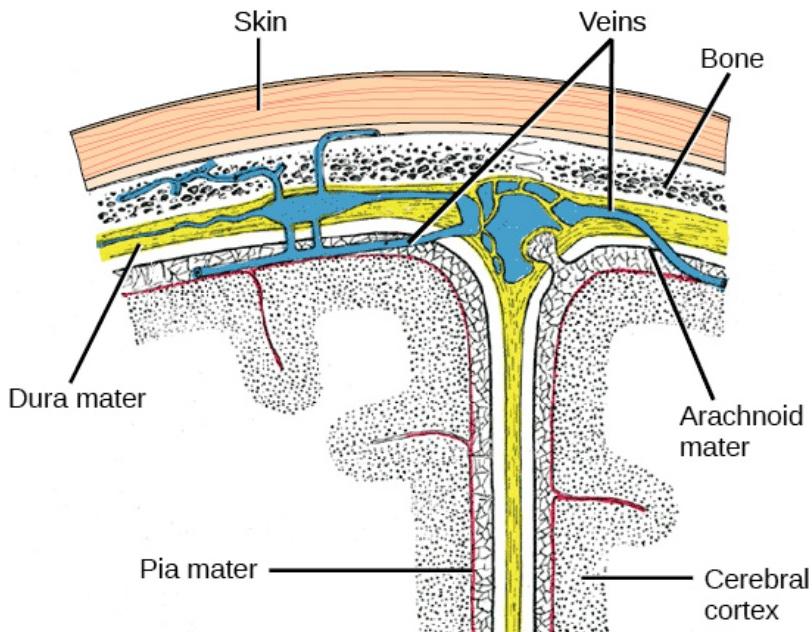
How Neurons Communicate

All functions performed by the nervous system—from a simple motor reflex to more advanced functions like making a memory or a decision—require neurons to communicate with one another. Neurons communicate between the axon of one neuron and the dendrites, and sometimes the cell body, of another neuron across the gap between them, known as the **synaptic cleft**. When an action potential reaches the end of an axon it stimulates the release of neurotransmitter molecules into the synaptic cleft between the synaptic knob of the axon and the post-synaptic membrane of the dendrite or soma of the next cell. The neurotransmitter is released through exocytosis of vesicles containing the neurotransmitter molecules. The neurotransmitter diffuses across the synaptic cleft

and binds to receptors in the post-synaptic membrane. These receptor molecules are chemically regulated ion channels and will open, allowing sodium to enter the cell. If sufficient neurotransmitter has been released an action potential may be initiated in the next cell, but this is not guaranteed. If insufficient neurotransmitter is released the nerve signal will die at this point. There are a number of different neurotransmitters that are specific to neuron types that have specific functions. The cerebral cortex is covered by three layers of meninges: the dura, arachnoid, and pia maters. (credit: modification of work by Gray's Anatomy)

The Central Nervous System

The **central nervous system (CNS)** is made up of the brain and spinal cord and is covered with three layers of protective coverings called **meninges** (“meninges” is derived from the Greek and means “membranes”) ([\[link\]](#)). The outermost layer is the dura mater, the middle layer is the web-like arachnoid mater, and the inner layer is the pia mater, which directly contacts and covers the brain and spinal cord. The space between the arachnoid and pia maters is filled with **cerebrospinal fluid (CSF)**. The brain floats in CSF, which acts as a cushion and shock absorber.



The human cerebral cortex includes the frontal, parietal, temporal, and occipital lobes.

The Brain

The brain is the part of the central nervous system that is contained in the cranial cavity of the skull. It includes the cerebral cortex, limbic system, basal ganglia, thalamus, hypothalamus, cerebellum, brainstem, and retinas. The outermost part of the brain is a thick piece of nervous system tissue called the **cerebral cortex**. The cerebral cortex, limbic system, and basal ganglia make up the two cerebral hemispheres. A thick fiber bundle called the **corpus callosum** (corpus = “body”; callosum = “tough”) connects the two hemispheres. Although there are some brain functions that are localized more to one

hemisphere than the other, the functions of the two hemispheres are largely redundant. In fact, sometimes (very rarely) an entire hemisphere is removed to treat severe epilepsy. While patients do suffer some deficits following the surgery, they can have surprisingly few problems, especially when the surgery is performed on children who have very immature nervous systems.

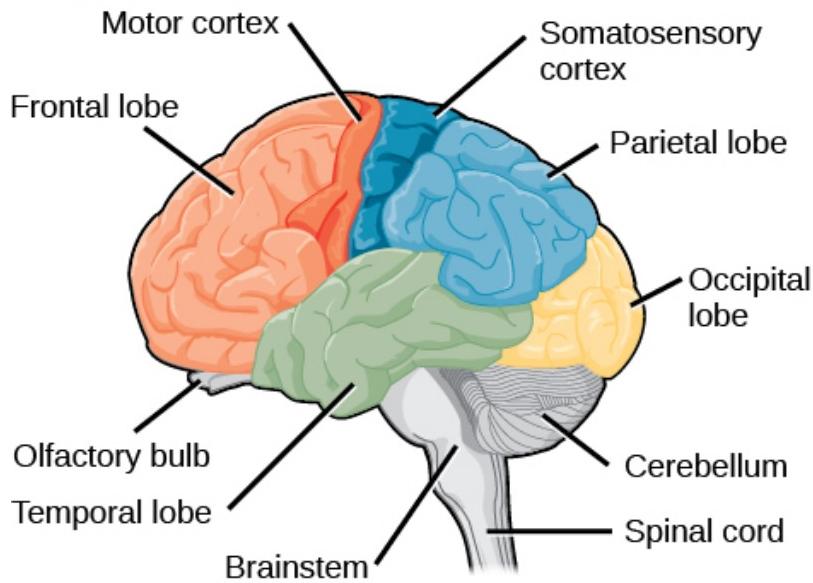
In other surgeries to treat severe epilepsy, the corpus callosum is cut instead of removing an entire hemisphere. This causes a condition called split-brain, which gives insights into unique functions of the two hemispheres. For example, when an object is presented to patients' left visual field, they may be unable to verbally name the object (and may claim to not have seen an object at all). This is because the visual input from the left visual field crosses and enters the right hemisphere and cannot then signal to the speech center, which generally is found in the left side of the brain. Remarkably, if a split-brain patient is asked to pick up a specific object out of a group of objects with the left hand, the patient will be able to do so but will still be unable to verbally identify it.

Concept in Action

Visit the following [website](#) to learn more about split-brain patients and to play a game where you

can model split-brain experiments yourself.

Each hemisphere contains regions called lobes that are involved in different functions. Each hemisphere of the mammalian cerebral cortex can be broken down into four functionally and spatially defined lobes: frontal, parietal, temporal, and occipital ([\[link\]](#)).



The **frontal lobe** is located at the front of the brain, over the eyes. This lobe contains the olfactory bulb, which processes smells. The frontal lobe also contains the motor cortex, which is important for planning and implementing movement. Areas within the motor cortex map to different muscle groups. Neurons in the frontal lobe also control cognitive

functions like maintaining attention, speech, and decision-making. Studies of humans who have damaged their frontal lobes show that parts of this area are involved in personality, socialization, and assessing risk. The **parietal lobe** is located at the top of the brain. Neurons in the parietal lobe are involved in speech and also reading. Two of the parietal lobe's main functions are processing somatosensation—touch sensations like pressure, pain, heat, cold—and processing proprioception—the sense of how parts of the body are oriented in space. The parietal lobe contains a somatosensory map of the body similar to the motor cortex. The **occipital lobe** is located at the back of the brain. It is primarily involved in vision—seeing, recognizing, and identifying the visual world. The **temporal lobe** is located at the base of the brain and is primarily involved in processing and interpreting sounds. It also contains the **hippocampus** (named from the Greek for “seahorse,” which it resembles in shape) a structure that processes memory formation. The role of the hippocampus in memory was partially determined by studying one famous epileptic patient, HM, who had both sides of his hippocampus removed in an attempt to cure his epilepsy. His seizures went away, but he could no longer form new memories (although he could remember some facts from before his surgery and could learn new motor tasks).

Interconnected brain areas called the **basal ganglia**

play important roles in movement control and posture. The basal ganglia also regulate motivation.

The **thalamus** acts as a gateway to and from the cortex. It receives sensory and motor inputs from the body and also receives feedback from the cortex. This feedback mechanism can modulate conscious awareness of sensory and motor inputs depending on the attention and arousal state of the animal. The thalamus helps regulate consciousness, arousal, and sleep states.

Below the thalamus is the **hypothalamus**. The hypothalamus controls the endocrine system by sending signals to the pituitary gland. Among other functions, the hypothalamus is the body's thermostat—it makes sure the body temperature is kept at appropriate levels. Neurons within the hypothalamus also regulate circadian rhythms, sometimes called sleep cycles.

The **limbic system** is a connected set of structures that regulates emotion, as well as behaviors related to fear and motivation. It plays a role in memory formation and includes parts of the thalamus and hypothalamus as well as the hippocampus. One important structure within the limbic system is a temporal lobe structure called the **amygdala**. The two amygdala (one on each side) are important both for the sensation of fear and for recognizing fearful faces.

The **cerebellum** (cerebellum = “little brain”) sits at the base of the brain on top of the brainstem. The cerebellum controls balance and aids in coordinating movement and learning new motor tasks. The cerebellum of birds is large compared to other vertebrates because of the coordination required by flight.

The **brainstem** connects the rest of the brain with the spinal cord and regulates some of the most important and basic functions of the nervous system including breathing, swallowing, digestion, sleeping, walking, and sensory and motor information integration.

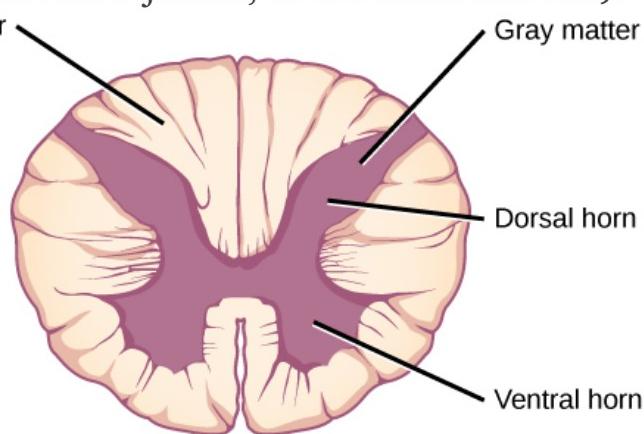
A cross-section of the spinal cord shows gray matter (containing cell bodies and interneurons) and white matter (containing myelinated axons).

Spinal cord

Connecting to the brainstem and extending down the body through the spinal column is the spinal cord. The spinal cord is a thick bundle of nerve tissue that carries information about the body to the brain and from the brain to the body. The spinal cord is contained within the meninges and the bones of the vertebral column but is able to communicate signals to and from the body through its connections with spinal nerves (part of the peripheral nervous system). A cross-section of the spinal cord looks like a white oval containing a gray butterfly-shape

([link]). Axons make up the “white matter” and neuron and glia cell bodies (and interneurons) make up the “gray matter.” Axons and cell bodies in the dorsal spinal cord convey mostly sensory information from the body to the brain. Axons and cell bodies in the spinal cord primarily transmit signals controlling movement from the brain to the body.

The spinal cord also controls motor reflexes. These reflexes are quick, unconscious movements—like automatically removing a hand from a hot object. Reflexes are so fast because they involve local synaptic connections. For example, the knee reflex that a doctor tests during a routine physical is controlled by a single synapse between a sensory neuron and a motor neuron. While a reflex may only require the involvement of one or two synapses, synapses with interneurons in the spinal column transmit information to the brain to convey what happened (the knee jerked, or the hand was hot).



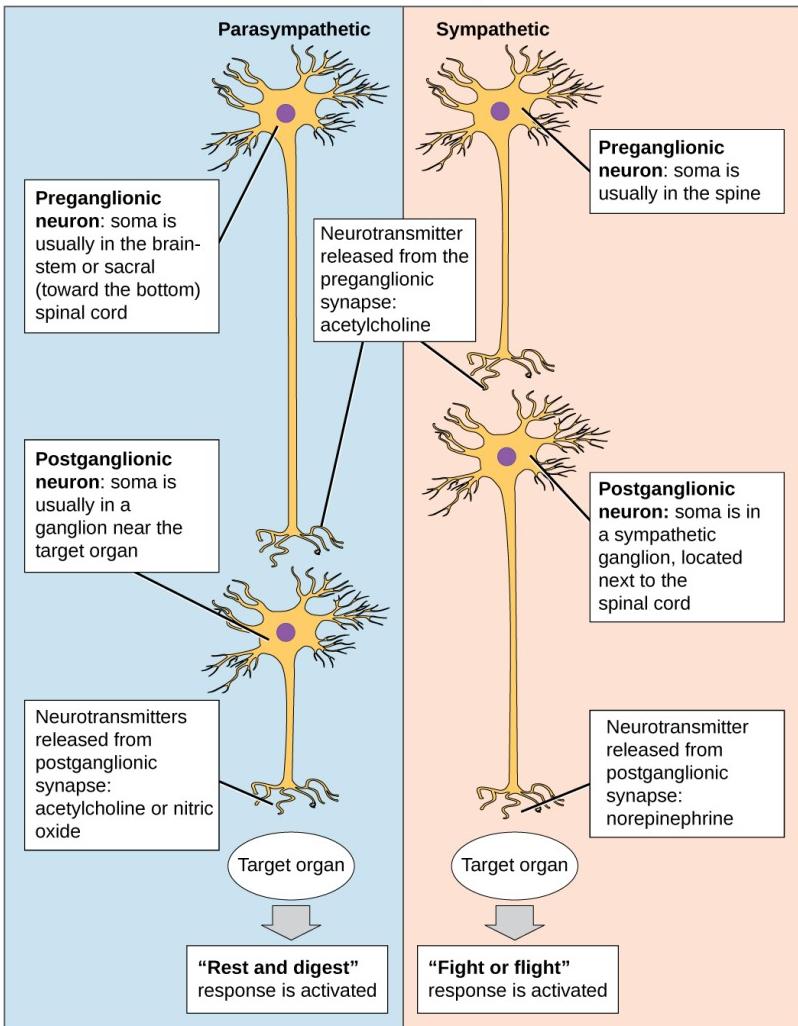
In the autonomic nervous system, a preganglionic

neuron (originating in the CNS) synapses to a neuron in a ganglion that, in turn, synapses on a target organ. Activation of the sympathetic nervous system causes release of norepinephrine on the target organ. Activation of the parasympathetic nervous system causes release of acetylcholine on the target organ. The sympathetic and parasympathetic nervous systems often have opposing effects on target organs.

The Peripheral Nervous System

The **peripheral nervous system (PNS)** is the connection between the central nervous system and the rest of the body. The PNS can be broken down into the **autonomic nervous system**, which controls bodily functions without conscious control, and the **sensory-somatic nervous system**, which transmits sensory information from the skin, muscles, and sensory organs to the CNS and sends motor commands from the CNS to the muscles.

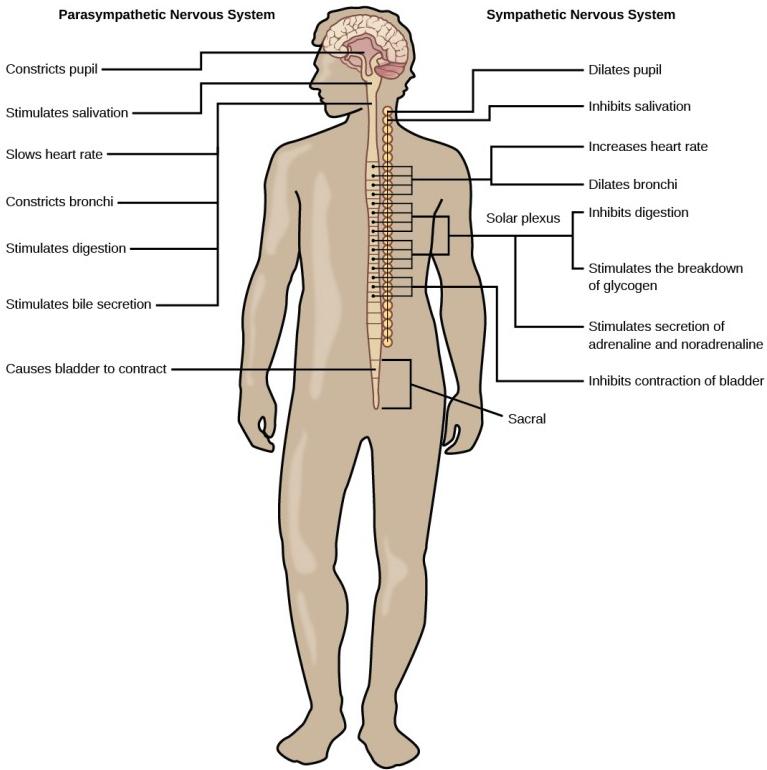
Autonomic Nervous System



The autonomic nervous system serves as the relay between the CNS and the internal organs. It controls the lungs, the heart, smooth muscle, and exocrine and endocrine glands. The autonomic nervous system controls these organs largely without conscious control; it can continuously monitor the conditions of these different systems and implement

changes as needed. Signaling to the target tissue usually involves two synapses: a preganglionic neuron (originating in the CNS) synapses to a neuron in a ganglion that, in turn, synapses on the target organ ([\[link\]](#)). There are two divisions of the autonomic nervous system that often have opposing effects: the sympathetic nervous system and the parasympathetic nervous system.

The **sympathetic nervous system** is responsible for the immediate responses an animal makes when it encounters a dangerous situation. One way to remember this is to think of the “fight-or-flight” response a person feels when encountering a snake (“snake” and “sympathetic” both begin with “s”). Examples of functions controlled by the sympathetic nervous system include an accelerated heart rate and inhibited digestion. These functions help prepare an organism’s body for the physical strain required to escape a potentially dangerous situation or to fend off a predator.



While the sympathetic nervous system is activated in stressful situations, the **parasympathetic nervous system** allows an animal to “rest and digest.” One way to remember this is to think that during a restful situation like a picnic, the parasympathetic nervous system is in control (“picnic” and “parasympathetic” both start with “p”). Parasympathetic preganglionic neurons have cell bodies located in the brainstem and in the sacral (toward the bottom) spinal cord ([\[link\]](#)). The parasympathetic nervous system resets organ function after the sympathetic nervous system is activated including slowing of heart rate, lowered

blood pressure, and stimulation of digestion.

The sensory-somatic nervous system is made up of cranial and spinal nerves and contains both sensory and motor neurons. Sensory neurons transmit sensory information from the skin, skeletal muscle, and sensory organs to the CNS. Motor neurons transmit messages about desired movement from the CNS to the muscles to make them contract. Without its sensory-somatic nervous system, an animal would be unable to process any information about its environment (what it sees, feels, hears, and so on) and could not control motor movements. Unlike the autonomic nervous system, which usually has two synapses between the CNS and the target organ, sensory and motor neurons usually have only one synapse—one ending of the neuron is at the organ and the other directly contacts a CNS neuron.

Section Summary

The nervous system is made up of neurons and glia. Neurons are specialized cells that are capable of sending electrical as well as chemical signals. Most neurons contain dendrites, which receive these signals, and axons that send signals to other neurons or tissues. Glia are non-neuronal cells in the nervous system that support neuronal development and signaling. There are several types of glia that serve different functions.

Neurons have a resting potential across their membranes and when they are stimulated by a strong enough signal from another neuron an action potential may carry an electrochemical signal along the neuron to a synapse with another neuron.

Neurotransmitters carry signals across synapses to initiate a response in another neuron.

The vertebrate central nervous system contains the brain and the spinal cord, which are covered and protected by three meninges. The brain contains structurally and functionally defined regions. In mammals, these include the cortex (which can be broken down into four primary functional lobes: frontal, temporal, occipital, and parietal), basal ganglia, thalamus, hypothalamus, limbic system, cerebellum, and brainstem—although structures in some of these designations overlap. While functions may be primarily localized to one structure in the brain, most complex functions, like language and sleep, involve neurons in multiple brain regions. The spinal cord is the information superhighway that connects the brain with the rest of the body through its connections with peripheral nerves. It transmits sensory and motor input and also controls motor reflexes.

The peripheral nervous system contains both the autonomic and sensory-somatic nervous systems. The autonomic nervous system provides unconscious control over visceral functions and has

two divisions: the sympathetic and parasympathetic nervous systems. The sympathetic nervous system is activated in stressful situations to prepare the animal for a “fight-or-flight” response. The parasympathetic nervous system is active during restful periods. The sensory-somatic nervous system is made of cranial and spinal nerves that transmit sensory information from skin and muscle to the CNS and motor commands from the CNS to the muscles.

Review Questions

Neurons contain _____, which can receive signals from other neurons.

1. axons
 2. mitochondria
 3. dendrites
 4. Golgi bodies
-

C

The part of the brain that is responsible for coordination during movement is the _____.

1. limbic system

-
- 2. thalamus
 - 3. cerebellum
 - 4. parietal lobe
-

C

Which part of the nervous system directly controls the digestive system?

- 1. parasympathetic nervous system
 - 2. central nervous system
 - 3. spinal cord
 - 4. sensory-somatic nervous system
-

A

Free Response

How are neurons similar to other cells? How are they unique?

Neurons contain organelles common to all cells, such as a nucleus and mitochondria. They are unique because they contain dendrites, which can receive signals from other neurons, and

axons that can send these signals to other cells.

What are the main functions of the spinal cord?

The spinal cord transmits sensory information from the body to the brain and motor commands from the brain to the body through its connections with peripheral nerves. It also controls motor reflexes.

What are the main differences between the sympathetic and parasympathetic branches of the autonomic nervous system?

The sympathetic nervous system prepares the body for “fight or flight,” whereas the parasympathetic nervous system allows the body to “rest and digest.” Sympathetic neurons release norepinephrine onto target organs; parasympathetic neurons release acetylcholine. Sympathetic neuron cell bodies are located in sympathetic ganglia. Parasympathetic neuron cell bodies are located in the brainstem and sacral spinal cord. Activation of the sympathetic nervous system increases heart rate and blood pressure and decreases digestion and blood flow to the skin. Activation of the parasympathetic nervous system decreases heart rate and blood

pressure and increases digestion and blood flow to the skin.

What are the main functions of the sensory-somatic nervous system?

The sensory-somatic nervous system transmits sensory information from the skin, muscles, and sensory organs to the CNS. It also sends motor commands from the CNS to the muscles, causing them to contract.

Glossary

action potential

a momentary change in the electrical potential of a neuron (or muscle) membrane

amygdala

a structure within the limbic system that processes fear

autonomic nervous system

the part of the peripheral nervous system that controls bodily functions

axon

a tube-like structure that propagates a signal from a neuron's cell body to axon terminals

basal ganglia

an interconnected collections of cells in the brain that are involved in movement and motivation

brainstem

a portion of brain that connects with the spinal cord; controls basic nervous system functions like breathing and swallowing

central nervous system (CNS)

the nervous system made up of the brain and spinal cord; covered with three layers of protective meninges

cerebellum

the brain structure involved in posture, motor coordination, and learning new motor actions

cerebral cortex

the outermost sheet of brain tissue; involved in many higher-order functions

cerebrospinal fluid (CSF)

a clear liquid that surrounds the brain and fills its ventricles and acts as a shock absorber

corpus callosum

a thick nerve bundle that connects the cerebral hemispheres

dendrite

a structure that extends away from the cell body to receive messages from other neurons

depolarization

a change in the membrane potential to a less negative value

frontal lobe

the part of the cerebral cortex that contains the motor cortex and areas involved in planning, attention, and language

glia

(also, glial cells) the cells that provide support functions for neurons

hippocampus

the brain structure in the temporal lobe involved in processing memories

hypothalamus

the brain structure that controls hormone release and body homeostasis

limbic system

a connected brain area that processes emotion and motivation

membrane potential

a difference in electrical potential between the inside and outside of a cell

meninges

(singular: meninx) the membranes that cover and protect the central nervous system

myelin sheath

a cellular extension containing a fatty substance produced by glia that surrounds and insulates axons

neuron

a specialized cell that can receive and transmit electrical and chemical signals

occipital lobe

the part of the cerebral cortex that contains visual cortex and processes visual stimuli

parasympathetic nervous system

the division of autonomic nervous system that regulates visceral functions during relaxation

parietal lobe

the part of the cerebral cortex involved in processing touch and the sense of the body in space

peripheral nervous system (PNS)

the nervous system that serves as the connection between the central nervous system and the rest of the body; consists of the autonomic nervous system and the sensory-somatic nervous system

sensory-somatic nervous system
the system of sensory and motor nerves

spinal cord

a thick fiber bundle that connects the brain with peripheral nerves; transmits sensory and motor information; contains neurons that control motor reflexes

sympathetic nervous system

the division of autonomic nervous system activated during stressful "fight-or-flight" situations

synapse

a junction between two neurons where neuronal signals are communicated

synaptic cleft

a space between the presynaptic and postsynaptic membranes

temporal lobe

the part of the cerebral cortex that processes auditory input; parts of the temporal lobe are involved in speech, memory, and emotion processing

thalamus

the brain area that relays sensory information to the cortex

threshold of excitation

the level of depolarization needed for an action potential to fire

Sensory Processes

By the end of this section, you will be able to do the following:

- Identify the general and special senses in humans
- Describe three important steps in sensory perception
- Explain the concept of just-noticeable difference in sensory perception

Senses provide information about the body and its environment. Humans have five special senses: olfaction (smell), gustation (taste), equilibrium (balance and body position), vision, and hearing. Additionally, we possess general senses, also called somatosensation, which respond to stimuli like temperature, pain, pressure, and vibration.

Vestibular sensation, which is an organism's sense of spatial orientation and balance, **proprioception** (position of bones, joints, and muscles), and the sense of limb position that is used to track **kinesthesia** (limb movement) are part of somatosensation. Although the sensory systems associated with these senses are very different, all share a common function: to convert a stimulus (such as light, or sound, or the position of the body) into an electrical signal in the nervous system. This process is called **sensory transduction**.

There are two broad types of cellular systems that

perform sensory transduction. In one, a neuron works with a **sensory receptor**, a cell, or cell process that is specialized to engage with and detect a specific stimulus. Stimulation of the sensory receptor activates the associated afferent neuron, which carries information about the stimulus to the central nervous system. In the second type of sensory transduction, a sensory nerve ending responds to a stimulus in the internal or external environment: this neuron constitutes the sensory receptor. Free nerve endings can be stimulated by several different stimuli, thus showing little receptor specificity. For example, pain receptors in your gums and teeth may be stimulated by temperature changes, chemical stimulation, or pressure.

Reception

The first step in sensation is **reception**, which is the activation of sensory receptors by stimuli such as mechanical stimuli (being bent or squished, for example), chemicals, or temperature. The receptor can then respond to the stimuli. The region in space in which a given sensory receptor can respond to a stimulus, be it far away or in contact with the body, is that receptor's **receptive field**. Think for a moment about the differences in receptive fields for the different senses. For the sense of touch, a stimulus must come into contact with the body. For the sense of hearing, a stimulus can be a moderate

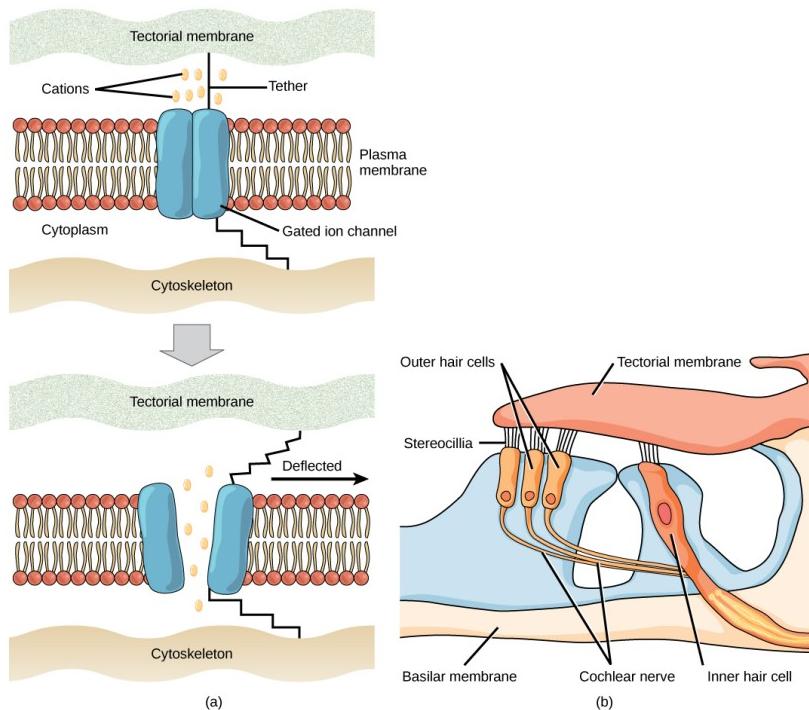
distance away (some baleen whale sounds can propagate for many kilometers). For vision, a stimulus can be very far away; for example, the visual system perceives light from stars at enormous distances.

(a) Mechanosensitive ion channels are gated ion channels that respond to mechanical deformation of the plasma membrane. A mechanosensitive channel is connected to the plasma membrane and the cytoskeleton by hair-like tethers. When pressure causes the extracellular matrix to move, the channel opens, allowing ions to enter or exit the cell. (b) Stereocilia in the human ear are connected to mechanosensitive ion channels. When a sound causes the stereocilia to move, mechanosensitive ion channels transduce the signal to the cochlear nerve.

Transduction

The most fundamental function of a sensory system is the translation of a sensory signal to an electrical signal in the nervous system. This takes place at the sensory receptor, and the change in electrical potential that is produced is called the **receptor potential**. How is sensory input, such as pressure on the skin, changed to a receptor potential? In this example, a type of receptor called a **mechanoreceptor** (as shown in [\[link\]](#)) possesses specialized membranes that respond to pressure. Disturbance of these dendrites by compressing them or bending them opens gated ion channels in the

plasma membrane of the sensory neuron, changing its electrical potential. Recall that in the nervous system, a positive change of a neuron's electrical potential (also called the membrane potential), depolarizes the neuron. Receptor potentials are graded potentials: the magnitude of these graded (receptor) potentials varies with the strength of the stimulus. If the magnitude of depolarization is sufficient (that is, if membrane potential reaches a threshold), the neuron will fire an action potential. In most cases, the correct stimulus impinging on a sensory receptor will drive membrane potential in a positive direction, although for some receptors, such as those in the visual system, this is not always the case.



Sensory receptors for different senses are very different from each other, and they are specialized according to the type of stimulus they sense: they have receptor specificity. For example, touch receptors, light receptors, and sound receptors are each activated by different stimuli. Touch receptors are not sensitive to light or sound; they are sensitive only to touch or pressure. However, stimuli may be combined at higher levels in the brain, as happens with olfaction, contributing to our sense of taste.

Encoding and Transmission of Sensory Information

Four aspects of sensory information are encoded by sensory systems: the type of stimulus, the location of the stimulus in the receptive field, the duration of the stimulus, and the relative intensity of the stimulus. Thus, action potentials transmitted over a sensory receptor's afferent axons encode one type of stimulus, and this segregation of the senses is preserved in other sensory circuits. For example, auditory receptors transmit signals over their own dedicated system, and electrical activity in the axons of the auditory receptors will be interpreted by the brain as an auditory stimulus—a sound.

The intensity of a stimulus is often encoded in the rate of action potentials produced by the sensory receptor. Thus, an intense stimulus will produce a more rapid train of action potentials, and reducing

the stimulus will likewise slow the rate of production of action potentials. A second way in which intensity is encoded is by the number of receptors activated. An intense stimulus might initiate action potentials in a large number of adjacent receptors, while a less intense stimulus might stimulate fewer receptors. Integration of sensory information begins as soon as the information is received in the CNS, and the brain will further process incoming signals.

In humans, with the exception of olfaction, all sensory signals are routed from the (a) thalamus to (b) final processing regions in the cortex of the brain. (credit b: modification of work by Polina Tishina)

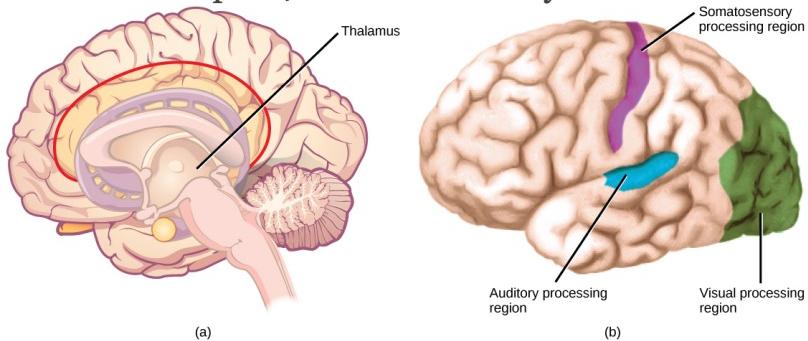
Perception

Perception is an individual's interpretation of a sensation. Although perception relies on the activation of sensory receptors, perception happens not at the level of the sensory receptor, but at higher levels in the nervous system, in the brain. The brain distinguishes sensory stimuli through a sensory pathway: action potentials from sensory receptors travel along neurons that are dedicated to a particular stimulus. These neurons are dedicated to that particular stimulus and synapse with particular neurons in the brain or spinal cord.

All sensory signals, except those from the olfactory

system, are transmitted through the central nervous system and are routed to the thalamus and to the appropriate region of the cortex. Recall that the thalamus is a structure in the forebrain that serves as a clearinghouse and relay station for sensory (as well as motor) signals. When the sensory signal exits the thalamus, it is conducted to the specific area of the cortex ([\[link\]](#)) dedicated to processing that particular sense.

How are neural signals interpreted? Interpretation of sensory signals between individuals of the same species is largely similar, owing to the inherited similarity of their nervous systems; however, there are some individual differences. A good example of this is individual tolerances to a painful stimulus, such as dental pain, which certainly differ.



Scientific Method Connection Just-Noticeable Difference

It is easy to differentiate between a one-pound bag of rice and a two-pound bag of rice. There is a one-

pound difference, and one bag is twice as heavy as the other. However, would it be as easy to differentiate between a 20- and a 21-pound bag?

Question: What is the smallest detectable weight difference between a one-pound bag of rice and a larger bag? What is the smallest detectable difference between a 20-pound bag and a larger bag? In both cases, at what weights are the differences detected? This smallest detectable difference in stimuli is known as the just-noticeable difference (JND).

Background: Research background literature on JND and on Weber's Law, a description of a proposed mathematical relationship between the overall magnitude of the stimulus and the JND. You will be testing JND of different weights of rice in bags. Choose a convenient increment that is to be stepped through while testing. For example, you could choose 10 percent increments between one and two pounds (1.1, 1.2, 1.3, 1.4, and so on) or 20 percent increments (1.2, 1.4, 1.6, and 1.8).

Hypothesis: Develop a hypothesis about JND in terms of percentage of the whole weight being tested (such as "the JND between the two small bags and between the two large bags is proportionally the same," or "... is not proportionally the same.") So, for the first hypothesis, if the JND between the one-pound bag and a larger bag is 0.2 pounds (that is, 20 percent; 1.0 pound feels the same as 1.1 pounds, but 1.0 pound feels less than 1.2 pounds), then the JND

between the 20-pound bag and a larger bag will also be 20 percent. (So, 20 pounds feels the same as 22 pounds or 23 pounds, but 20 pounds feels less than 24 pounds.)

Test the hypothesis: Enlist 24 participants, and split them into two groups of 12. To set up the demonstration, assuming a 10 percent increment was selected, have the first group be the one-pound group. As a counter-balancing measure against a systematic error, however, six of the first group will compare one pound to two pounds, and step down in weight (1.0 to 2.0, 1.0 to 1.9, and so on), while the other six will step up (1.0 to 1.1, 1.0 to 1.2, and so on). Apply the same principle to the 20-pound group (20 to 40, 20 to 38, and so on, and 20 to 22, 20 to 24, and so on). Given the large difference between 20 and 40 pounds, you may wish to use 30 pounds as your larger weight. In any case, use two weights that are easily detectable as different.

Record the observations: Record the data in a table similar to the table below. For the one-pound and 20-pound groups (base weights) record a plus sign (+) for each participant that detects a difference between the base weight and the step weight. Record a minus sign (-) for each participant that finds no difference. If one-tenth steps were not used, then replace the steps in the “Step Weight” columns with the step you are using.

**Results of
JND
Testing (+
=
difference;
- = no
difference)**

Step Weight	One pound	20 pounds	Step Weight
1.1			22
1.2			24
1.3			26
1.4			28
1.5			30
1.6			32
1.7			34
1.8			36
1.9			38
2.0			40

Analyze the data/report the results: What step weight did all participants find to be equal with one-pound base weight? What about the 20-pound group?

Draw a conclusion: Did the data support the hypothesis? Are the final weights proportionally the same? If not, why not? Do the findings adhere to Weber's Law? Weber's Law states that the concept that a just-noticeable difference in a stimulus is proportional to the magnitude of the original stimulus.

Section Summary

A sensory activation occurs when a physical or chemical stimulus is processed into a neural signal (sensory transduction) by a sensory receptor.

Perception is an individual interpretation of a sensation and is a brain function. Humans have special senses: olfaction, gustation, equilibrium, and hearing, plus the general senses of somatosensation.

Sensory receptors are either specialized cells associated with sensory neurons or the specialized ends of sensory neurons that are a part of the peripheral nervous system, and they are used to receive information about the environment (internal or external). Each sensory receptor is modified for the type of stimulus it detects. For example, neither gustatory receptors nor auditory receptors are sensitive to light. Each sensory receptor is responsive to stimuli within a specific region in space, which is known as that receptor's receptive field. The most fundamental function of a sensory system is the translation of a sensory signal to an electrical signal in the nervous system.

All sensory signals, except those from the olfactory system, enter the central nervous system and are routed to the thalamus. When the sensory signal exits the thalamus, it is conducted to the specific

area of the cortex dedicated to processing that particular sense.

Review Questions

Where does perception occur?

1. spinal cord
 2. cerebral cortex
 3. receptors
 4. thalamus
-

B

If a person's cold receptors no longer convert cold stimuli into sensory signals, that person has a problem with the process of _____.

1. reception
 2. transmission
 3. perception
 4. transduction
-

D

After somatosensory transduction, the sensory signal travels through the brain as a(n) _____ signal.

1. electrical
 2. pressure
 3. optical
 4. thermal
-

A

Many people experience motion sickness while traveling in a car. This sensation results from contradictory inputs arising from which senses?

1. Proprioception and Kinesthesia
 2. Somatosensation and Equilibrium
 3. Gustation and Vibration
 4. Vision and Vestibular System
-

D

Critical Thinking Questions

If a person sustains damage to axons leading

from sensory receptors to the central nervous system, which step or steps of sensory perception will be affected?

Transmission of sensory information from the receptor to the central nervous system will be impaired, and thus, perception of stimuli, which occurs in the brain, will be halted.

In what way does the overall magnitude of a stimulus affect the just-noticeable difference in the perception of that stimulus?

The just-noticeable difference is a fraction of the overall magnitude of the stimulus and seems to be a relatively fixed proportion (such as 10 percent) whether the stimulus is large (such as a very heavy object) or small (such as a very light object).

Describe the difference in the localization of the sensory receptors for general and special senses in humans.

General sensory receptors are located throughout the body in the skin and internal organs. Conversely, special senses are all

located in the head region, and require specialized organs.

Glossary

kinesthesia

sense of body movement

mechanoreceptor

sensory receptor modified to respond to mechanical disturbance such as being bent, touch, pressure, motion, and sound

perception

individual interpretation of a sensation; a brain function

proprioception

sense of limb position; used to track kinesthesia

reception

receipt of a signal (such as light or sound) by sensory receptors

receptive field

region in space in which a stimulus can activate a given sensory receptor

receptor potential

membrane potential in a sensory receptor in

response to detection of a stimulus

sensory receptor

specialized neuron or other cells associated with a neuron that is modified to receive specific sensory input

sensory transduction

conversion of a sensory stimulus into electrical energy in the nervous system by a change in the membrane potential

vestibular sense

sense of spatial orientation and balance

Somatosensation

By the end of this section, you will be able to do the following:

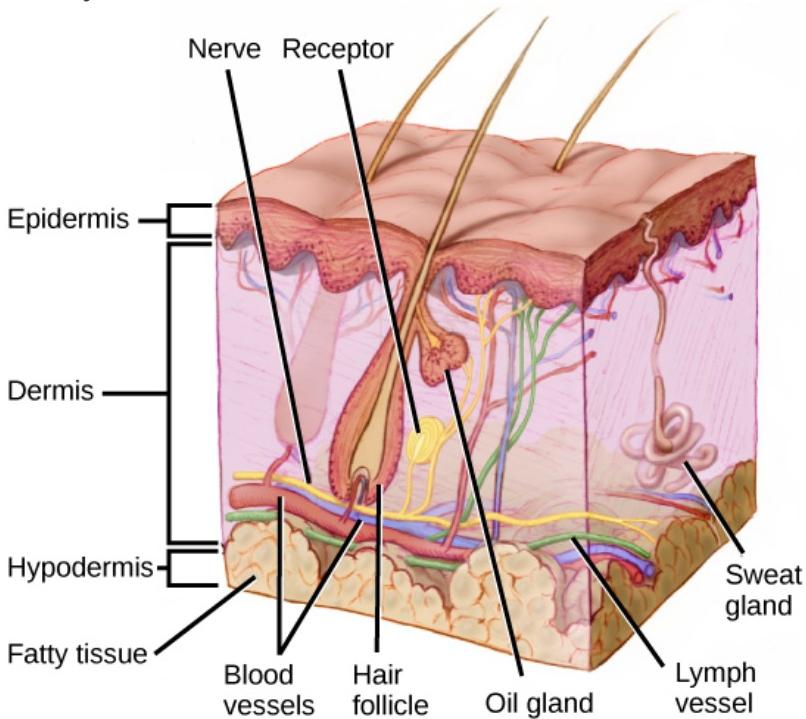
- Describe four important mechanoreceptors in human skin
- Describe the topographical distribution of somatosensory receptors between glabrous and hairy skin
- Explain why the perception of pain is subjective

Somatosensation is a mixed sensory category and includes all sensation received from the skin and mucous membranes, as well from as the limbs and joints. Somatosensation is also known as tactile sense, or more familiarly, as the sense of touch. Somatosensation occurs all over the exterior of the body and at some interior locations as well. A variety of receptor types—embedded in the skin, mucous membranes, muscles, joints, internal organs, and cardiovascular system—play a role.

Recall that the epidermis is the outermost layer of skin in mammals. It is relatively thin, is composed of keratin-filled cells, and has no blood supply. The epidermis serves as a barrier to water and to invasion by pathogens. Below this, the much thicker dermis contains blood vessels, sweat glands, hair follicles, lymph vessels, and lipid-secreting sebaceous glands ([\[link\]](#)). Below the epidermis and

dermis is the subcutaneous tissue, or hypodermis, the fatty layer that contains blood vessels, connective tissue, and the axons of sensory neurons. The hypodermis, which holds about 50 percent of the body's fat, attaches the dermis to the bone and muscle, and supplies nerves and blood vessels to the dermis.

Mammalian skin has three layers: an epidermis, a dermis, and a hypodermis. (credit: modification of work by Don Bliss, National Cancer Institute)



Meissner corpuscles in the fingertips, such as the one viewed here using bright field light microscopy, allow for touch discrimination of fine detail. (credit: modification of work by "Wbensmith"/Wikimedia Commons; scale-bar data from Matt Russell)

Pacinian corpuscles, such as these visualized using bright field light microscopy, detect pressure (touch) and high-frequency vibration. (credit: modification of work by Ed Uthman; scale-bar data from Matt Russell)

Somatosensory Receptors

Sensory receptors are classified into five categories: mechanoreceptors, thermoreceptors, proprioceptors, pain receptors, and chemoreceptors. These categories are based on the nature of stimuli each receptor class transduces. What is commonly referred to as “touch” involves more than one kind of stimulus and more than one kind of receptor. Mechanoreceptors in the skin are described as encapsulated (that is, surrounded by a capsule) or unencapsulated (a group that includes free nerve endings). A **free nerve ending**, as its name implies, is an unencapsulated dendrite of a sensory neuron. Free nerve endings are the most common nerve endings in skin, and they extend into the middle of the epidermis. Free nerve endings are sensitive to painful stimuli, to hot and cold, and to light touch. They are slow to adjust to a stimulus and so are less sensitive to abrupt changes in stimulation.

There are three classes of mechanoreceptors: tactile, proprioceptors, and baroreceptors. Mechanoreceptors sense stimuli due to physical deformation of their plasma membranes. They

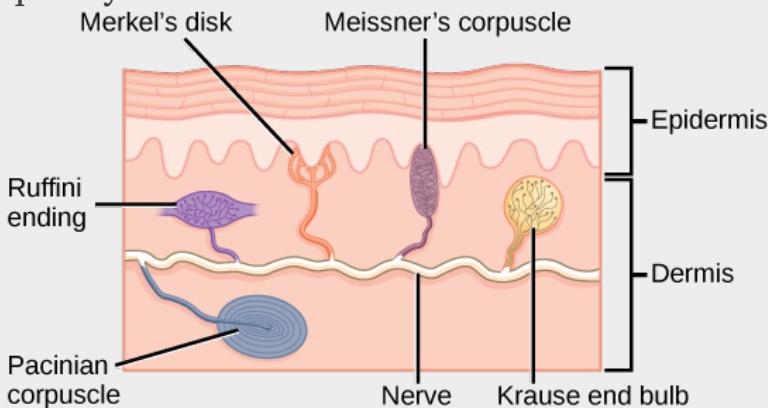
contain mechanically gated ion channels whose gates open or close in response to pressure, touch, stretching, and sound.” There are four primary tactile mechanoreceptors in human skin: Merkel’s disks, Meissner’s corpuscles, Ruffini endings, and Pacinian corpuscles; two are located toward the surface of the skin and two are located deeper. A fifth type of mechanoreceptor, Krause end bulbs, are found only in specialized regions. **Merkel’s disks** (shown in [\[link\]](#)) are found in the upper layers of skin near the base of the epidermis, both in skin that has hair and on **glabrous** skin, that is, the hairless skin found on the palms and fingers, the soles of the feet, and the lips of humans and other primates. Merkel’s disks are densely distributed in the fingertips and lips. They are slow-adapting, encapsulated nerve endings, and they respond to light touch. Light touch, also known as discriminative touch, is a light pressure that allows the location of a stimulus to be pinpointed. The receptive fields of Merkel’s disks are small with well-defined borders. That makes them finely sensitive to edges and they come into use in tasks such as typing on a keyboard.

Visual Connection

Four of the primary mechanoreceptors in human skin are shown. Merkel’s disks, which are unencapsulated, respond to light touch. Meissner’s

corpuscles, Ruffini endings, Pacinian corpuscles, and Krause end bulbs are all encapsulated.

Meissner's corpuscles respond to touch and low-frequency vibration. Ruffini endings detect stretch, deformation within joints, and warmth. Pacinian corpuscles detect transient pressure and high-frequency vibration. Krause end bulbs detect cold.

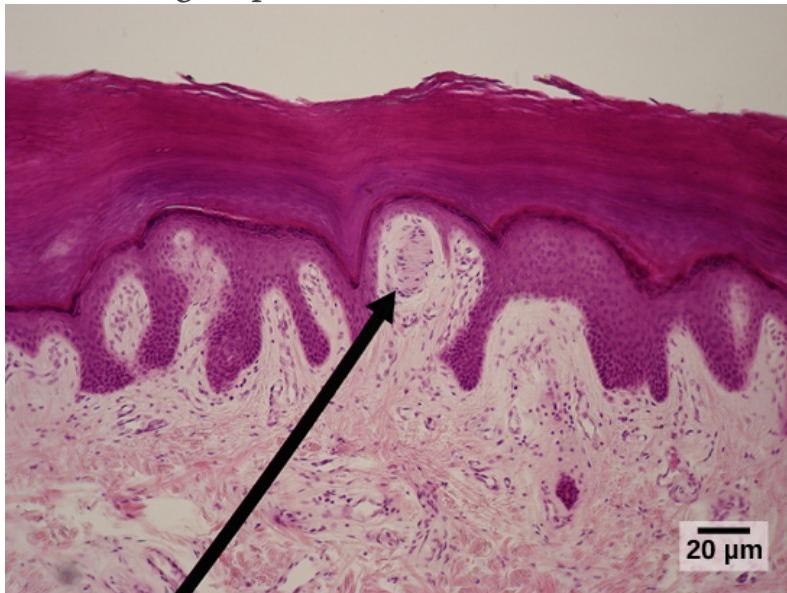


Which of the following statements about mechanoreceptors is false?

1. Pacinian corpuscles are found in both glabrous and hairy skin.
2. Merkel's disks are abundant on the fingertips and lips.
3. Ruffini endings are encapsulated mechanoreceptors.
4. Meissner's corpuscles extend into the lower dermis.

Meissner's corpuscles, (shown in [\[link\]](#)) also

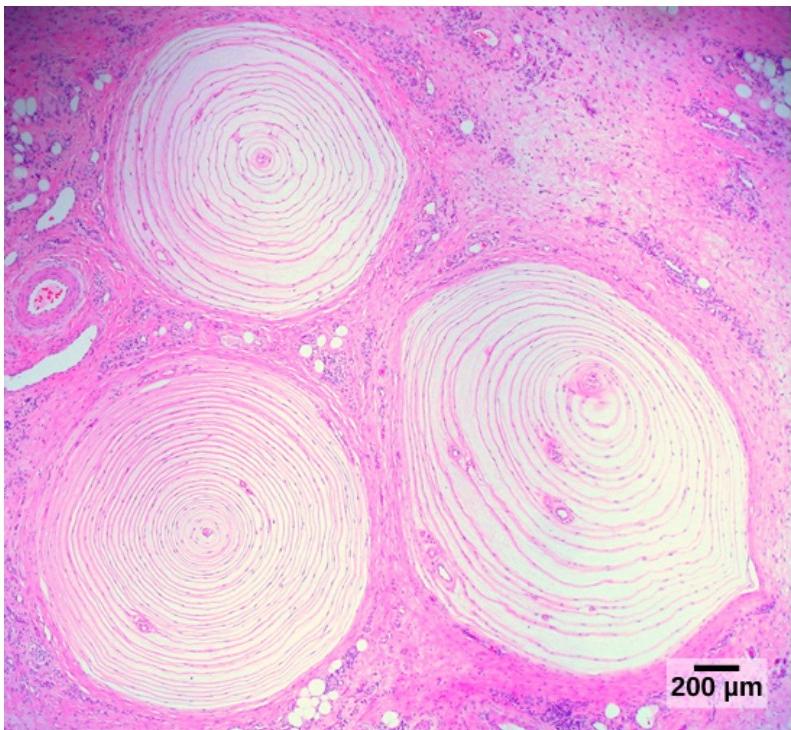
known as tactile corpuscles, are found in the upper dermis, but they project into the epidermis. They, too, are found primarily in the glabrous skin on the fingertips and eyelids. They respond to fine touch and pressure, but they also respond to low-frequency vibration or flutter. They are rapidly adapting, fluid-filled, encapsulated neurons with small, well-defined borders and are responsive to fine details. Like Merkel's disks, Meissner's corpuscles are not as plentiful in the palms as they are in the fingertips.



Deeper in the epidermis, near the base, are **Ruffini endings**, which are also known as bulbous corpuscles. They are found in both glabrous and hairy skin. These are slow-adapting, encapsulated mechanoreceptors that detect skin stretch and deformations within joints, so they provide valuable

feedback for gripping objects and controlling finger position and movement. Thus, they also contribute to proprioception and kinesthesia. Ruffini endings also detect warmth. Note that these warmth detectors are situated deeper in the skin than are the cold detectors. It is not surprising, then, that humans detect cold stimuli before they detect warm stimuli.

Pacinian corpuscles (seen in [\[link\]](#)) are located deep in the dermis of both glabrous and hairy skin and are structurally similar to Meissner's corpuscles; they are found in the bone periosteum, joint capsules, pancreas and other viscera, breast, and genitals. They are rapidly adapting mechanoreceptors that sense deep transient (but not prolonged) pressure and high-frequency vibration. Pacinian receptors detect pressure and vibration by being compressed, stimulating their internal dendrites. There are fewer Pacinian corpuscles and Ruffini endings in skin than there are Merkel's disks and Meissner's corpuscles.



In proprioception, proprioceptive and kinesthetic signals travel through myelinated afferent neurons running from the spinal cord to the medulla. Neurons are not physically connected, but communicate via neurotransmitters secreted into synapses or “gaps” between communicating neurons. Once in the medulla, the neurons continue carrying the signals to the thalamus.

Muscle spindles are stretch receptors that detect the amount of stretch, or lengthening of muscles. Related to these are **Golgi tendon organs**, which are tension receptors that detect the force of muscle contraction. Proprioceptive and kinesthetic signals

come from limbs. Unconscious proprioceptive signals run from the spinal cord to the cerebellum, the brain region that coordinates muscle contraction, rather than to the thalamus, like most other sensory information.

Baroreceptors detect pressure changes in an organ. They are found in the walls of the carotid artery and the aorta where they monitor blood pressure, and in the lungs where they detect the degree of lung expansion. Stretch receptors are found at various sites in the digestive and urinary systems.

In addition to these two types of deeper receptors, there are also rapidly adapting hair receptors, which are found on nerve endings that wrap around the base of hair follicles. There are a few types of hair receptors that detect slow and rapid hair movement, and they differ in their sensitivity to movement. Some hair receptors also detect skin deflection, and certain rapidly adapting hair receptors allow detection of stimuli that have not yet touched the skin.

Integration of Signals from Mechanoreceptors

The configuration of the different types of receptors working in concert in human skin results in a very refined sense of touch. The nociceptive receptors—those that detect pain—are located near the surface. Small, finely calibrated mechanoreceptors—Merkel's

disks and Meissner's corpuscles—are located in the upper layers and can precisely localize even gentle touch. The large mechanoreceptors—Pacinian corpuscles and Ruffini endings—are located in the lower layers and respond to deeper touch. (Consider that the deep pressure that reaches those deeper receptors would not need to be finely localized.) Both the upper and lower layers of the skin hold rapidly and slowly adapting receptors. Both primary somatosensory cortex and secondary cortical areas are responsible for processing the complex picture of stimuli transmitted from the interplay of mechanoreceptors.

Density of Mechanoreceptors

The distribution of touch receptors in human skin is not consistent over the body. In humans, touch receptors are less dense in skin covered with any type of hair, such as the arms, legs, torso, and face. Touch receptors are denser in glabrous skin (the type found on human fingertips and lips, for example), which is typically more sensitive and is thicker than hairy skin (4 to 5 mm versus 2 to 3 mm).

How is receptor density estimated in a human subject? The relative density of pressure receptors in different locations on the body can be demonstrated experimentally using a two-point discrimination test. In this demonstration, two sharp points, such as

two thumbtacks, are brought into contact with the subject's skin (though not hard enough to cause pain or break the skin). The subject reports if he or she feels one point or two points. If the two points are felt as one point, it can be inferred that the two points are both in the receptive field of a single sensory receptor. If two points are felt as two separate points, each is in the receptive field of two separate sensory receptors. The points could then be moved closer and retested until the subject reports feeling only one point, and the size of the receptive field of a single receptor could be estimated from that distance.

Thermoreception

In addition to Krause end bulbs that detect cold and Ruffini endings that detect warmth, there are different types of cold receptors on some free nerve endings: thermoreceptors, located in the dermis, skeletal muscles, liver, and hypothalamus, that are activated by different temperatures. Their pathways into the brain run from the spinal cord through the thalamus to the primary somatosensory cortex. Warmth and cold information from the face travels through one of the cranial nerves to the brain. You know from experience that a tolerably cold or hot stimulus can quickly progress to a much more intense stimulus that is no longer tolerable. Any stimulus that is too intense can be perceived as pain

because temperature sensations are conducted along the same pathways that carry pain sensations.

Pain

Pain is the name given to **nociception**, which is the neural processing of injurious stimuli in response to tissue damage. Pain is caused by true sources of injury, such as contact with a heat source that causes a thermal burn or contact with a corrosive chemical. But pain also can be caused by harmless stimuli that mimic the action of damaging stimuli, such as contact with capsaicins, the compounds that cause peppers to taste hot and which are used in self-defense pepper sprays and certain topical medications. Peppers taste “hot” because the protein receptors that bind capsaicin open the same calcium channels that are activated by warm receptors.

Nociception starts at the sensory receptors, but pain, inasmuch as it is the perception of nociception, does not start until it is communicated to the brain. There are several nociceptive pathways to and through the brain. Most axons carrying nociceptive information into the brain from the spinal cord project to the thalamus (as do other sensory neurons) and the neural signal undergoes final processing in the primary somatosensory cortex. Interestingly, one nociceptive pathway projects not to the thalamus but directly to the hypothalamus in

the forebrain, which modulates the cardiovascular and neuroendocrine functions of the autonomic nervous system. Recall that threatening—or painful—stimuli stimulate the sympathetic branch of the visceral sensory system, readying a fight-or-flight response.

Link to Learning

View this [video](#) that animates the five phases of nociceptive pain.

<https://www.openstax.org/l/nociceptive>

Section Summary

Somatosensation includes all sensation received from the skin and mucous membranes, as well as from the limbs and joints. Somatosensation occurs all over the exterior of the body and at some interior locations as well, and a variety of receptor types, embedded in the skin and mucous membranes, play a role.

There are several types of specialized sensory receptors. Rapidly adapting free nerve endings detect nociception, hot and cold, and light touch.

Slowly adapting, encapsulated Merkel's disks are found in fingertips and lips, and respond to light touch. Meissner's corpuscles, found in glabrous skin, are rapidly adapting, encapsulated receptors that detect touch, low-frequency vibration, and flutter. Ruffini endings are slowly adapting, encapsulated receptors that detect skin stretch, joint activity, and warmth. Hair receptors are rapidly adapting nerve endings wrapped around the base of hair follicles that detect hair movement and skin deflection. Finally, Pacinian corpuscles are encapsulated, rapidly adapting receptors that detect transient pressure and high-frequency vibration.

Visual Connection Questions

[\[link\]](#) Which of the following statements about mechanoreceptors is false?

1. Pacini corpuscles are found in both glabrous and hairy skin.
 2. Merkel's disks are abundant on the fingertips and lips.
 3. Ruffini endings are encapsulated mechanoreceptors.
 4. Meissner's corpuscles extend into the lower dermis.
-

[link] D

Review Questions

___ are found only in ___ skin, and detect skin deflection.

1. Meissner's corpuscles; hairy
 2. Merkel's disks; glabrous
 3. hair receptors; hairy
 4. Krause end bulbs; hairy
-

B

If you were to burn your epidermis, what receptor type would you most likely burn?

1. free nerve endings
 2. Ruffini endings
 3. Pacinian corpuscle
 4. hair receptors
-

A

Many diabetic patients are warned by their

doctors to test their glucose levels by pricking the sides of their fingers rather than the pads. Pricking the sides avoids stimulating which receptor?

1. Krause end bulbs
 2. Meissner's corpuscles
 3. Ruffini ending
 4. Nociceptors
-

B

Critical Thinking Questions

What can be inferred about the relative sizes of the areas of cortex that process signals from skin not densely innervated with sensory receptors and skin that is densely innervated with sensory receptors?

The cortical areas serving skin that is densely innervated likely are larger than those serving skin that is less densely innervated.

Many studies have demonstrated that women

are able to tolerate the same painful stimuli for longer than men. Why don't all people experience pain the same way?

Pain is a subjective sensation that relies on the brain interpreting the nociception signals received by the sensory receptors (perception). Therefore, even though two people experience identical stimuli, their brains can perceive them as very different sensory experiences.

Glossary

free nerve ending

ending of an afferent neuron that lacks a specialized structure for detection of sensory stimuli; some respond to touch, pain, or temperature

glabrous

describes the non-hairy skin found on palms and fingers, soles of feet, and lips of humans and other primates

Golgi tendon organ

muscular proprioceptive tension receptor that provides the sensory component of the Golgi tendon reflex

Meissner's corpuscle

(also, tactile corpuscle) encapsulated, rapidly-adapting mechanoreceptor in the skin that responds to light touch

Merkel's disk

unencapsulated, slowly-adapting mechanoreceptor in the skin that responds to touch

muscle spindle

proprioceptive stretch receptor that lies within a muscle and that shortens the muscle to an optimal length for efficient contraction

nociception

neural processing of noxious (such as damaging) stimuli

Pacinian corpuscle

encapsulated mechanoreceptor in the skin that responds to deep pressure and vibration

Ruffini ending

(also, bulbous corpuscle) slowly-adapting mechanoreceptor in the skin that responds to skin stretch and joint position

Vision

By the end of this section, you will be able to:

- Describe the basic anatomy of the visual system
- Discuss how rods and cones contribute to different aspects of vision
- Describe how monocular and binocular cues are used in the perception of depth

The visual system constructs a mental representation of the world around us ([\[link\]](#)). This contributes to our ability to successfully navigate through physical space and interact with important individuals and objects in our environments. This section will provide an overview of the basic anatomy and function of the visual system. In addition, we will explore our ability to perceive color and depth.

Our eyes take in sensory information that helps us understand the world around us. (credit "top left": modification of work by "rajkumar1220"/Flickr; credit "top right": modification of work by Thomas Leuthard; credit "middle left": modification of work by Demietrich Baker; credit "middle right": modification of work by "kaybee07"/Flickr; credit "bottom left": modification of work by "Isengardt"/Flickr; credit "bottom right": modification of work by Willem Heerbaart)

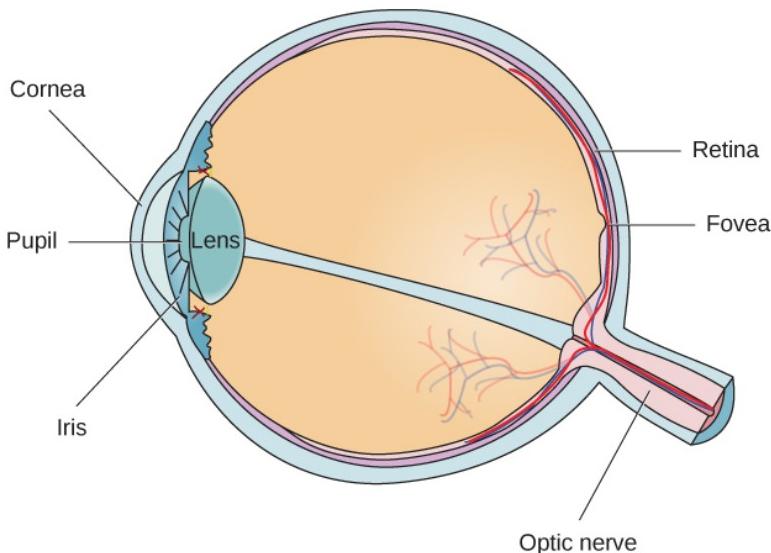


The anatomy of the eye is illustrated in this diagram. The two types of photoreceptors are shown in this image. Cones are colored green and rods are blue. This illustration shows the optic chiasm at the front of the brain and the pathways to the occipital lobe at the back of the brain, where visual sensations are processed into meaningful perceptions.

ANATOMY OF THE VISUAL SYSTEM

The eye is the major sensory organ involved in vision ([\[link\]](#)). Light waves are transmitted across the cornea and enter the eye through the pupil. The **cornea** is the transparent covering over the eye. It serves as a barrier between the inner eye and the outside world, and it is involved in focusing light waves that enter the eye. The **pupil** is the small opening in the eye through which light passes, and the size of the pupil can change as a function of light levels as well as emotional arousal. When light

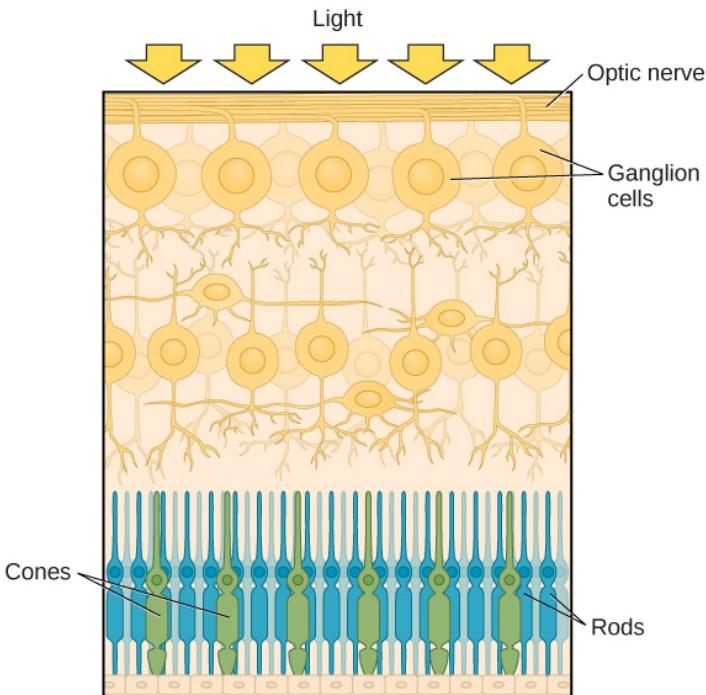
levels are low, the pupil will become dilated, or expanded, to allow more light to enter the eye. When light levels are high, the pupil will constrict, or become smaller, to reduce the amount of light that enters the eye. The pupil's size is controlled by muscles that are connected to the **iris**, which is the colored portion of the eye.



After passing through the pupil, light crosses the **lens**, a curved, transparent structure that serves to provide additional focus. The lens is attached to muscles that can change its shape to aid in focusing light that is reflected from near or far objects. In a normal-sighted individual, the lens will focus images perfectly on a small indentation in the back of the eye known as the **fovea**, which is part of the **retina**, the light-sensitive lining of the eye. The fovea contains densely packed specialized photoreceptor cells ([\[link\]](#)). These photoreceptor

cells, known as cones, are light-detecting cells. The **cones** are specialized types of photoreceptors that work best in bright light conditions. Cones are very sensitive to acute detail and provide tremendous spatial resolution. They also are directly involved in our ability to perceive color.

While cones are concentrated in the fovea, where images tend to be focused, rods, another type of photoreceptor, are located throughout the remainder of the retina. **Rods** are specialized photoreceptors that work well in low light conditions, and while they lack the spatial resolution and color function of the cones, they are involved in our vision in dimly lit environments as well as in our perception of movement on the periphery of our visual field.

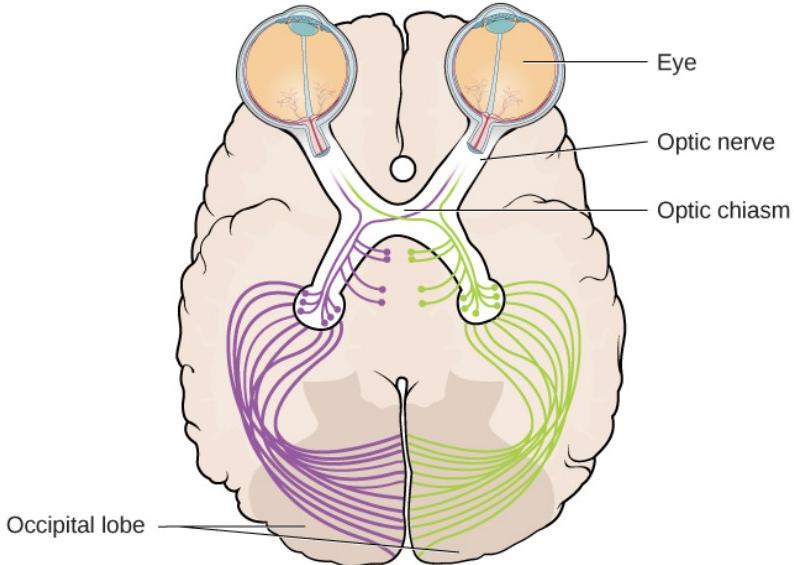


We have all experienced the different sensitivities of rods and cones when making the transition from a brightly lit environment to a dimly lit environment. Imagine going to see a blockbuster movie on a clear summer day. As you walk from the brightly lit lobby into the dark theater, you notice that you immediately have difficulty seeing much of anything. After a few minutes, you begin to adjust to the darkness and can see the interior of the theater. In the bright environment, your vision was dominated primarily by cone activity. As you move to the dark environment, rod activity dominates, but there is a delay in transitioning between the phases. If your rods do not transform light into nerve impulses as easily and efficiently as they should,

you will have difficulty seeing in dim light, a condition known as night blindness.

Rods and cones are connected (via several interneurons) to retinal ganglion cells. Axons from the retinal ganglion cells converge and exit through the back of the eye to form the **optic nerve**. The optic nerve carries visual information from the retina to the brain. There is a point in the visual field called the **blind spot**: Even when light from a small object is focused on the blind spot, we do not see it. We are not consciously aware of our blind spots for two reasons: First, each eye gets a slightly different view of the visual field; therefore, the blind spots do not overlap. Second, our visual system fills in the blind spot so that although we cannot respond to visual information that occurs in that portion of the visual field, we are also not aware that information is missing.

The optic nerve from each eye merges just below the brain at a point called the **optic chiasm**. As [\[link\]](#) shows, the optic chiasm is an X-shaped structure that sits just below the cerebral cortex at the front of the brain. At the point of the optic chiasm, information from the right visual field (which comes from both eyes) is sent to the left side of the brain, and information from the left visual field is sent to the right side of the brain.



Once inside the brain, visual information is sent via a number of structures to the occipital lobe at the back of the brain for processing. Visual information might be processed in parallel pathways which can generally be described as the “what pathway” and the “where/how” pathway. The “what pathway” is involved in object recognition and identification, while the “where/how pathway” is involved with location in space and how one might interact with a particular visual stimulus (Milner & Goodale, 2008; Ungerleider & Haxby, 1994). For example, when you see a ball rolling down the street, the “what pathway” identifies what the object is, and the “where/how pathway” identifies its location or movement in space.

This figure illustrates the different sensitivities for the three cone types found in a normal-sighted

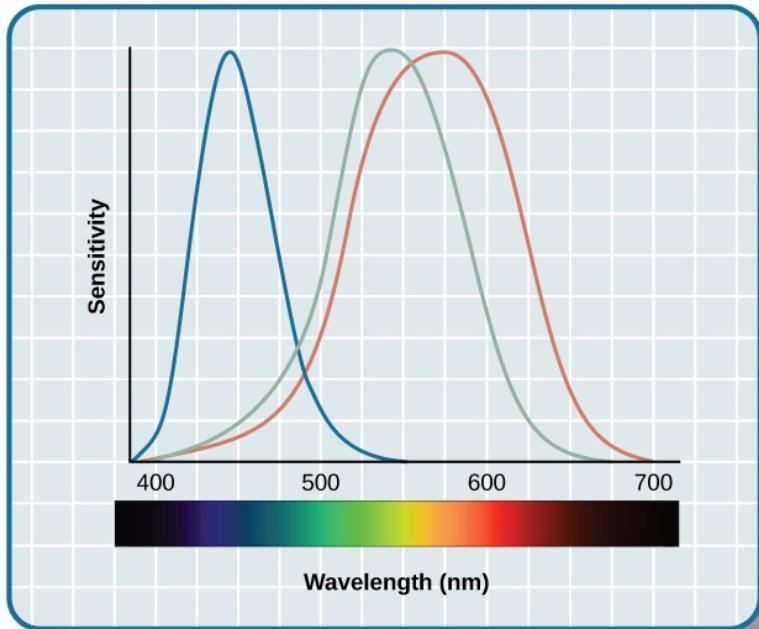
individual. (credit: modification of work by Vanessa Ezekowitz) Stare at the white dot for 30–60 seconds and then move your eyes to a blank piece of white paper. What do you see? This is known as a negative afterimage, and it provides empirical support for the opponent-process theory of color vision. We perceive depth in a two-dimensional figure like this one through the use of monocular cues like linear perspective, like the parallel lines converging as the road narrows in the distance. (credit: Marc Dalmulder)

COLOR AND DEPTH PERCEPTION

We do not see the world in black and white; neither do we see it as two-dimensional (2-D) or flat (just height and width, no depth). Let's look at how color vision works and how we perceive three dimensions (height, width, and depth).

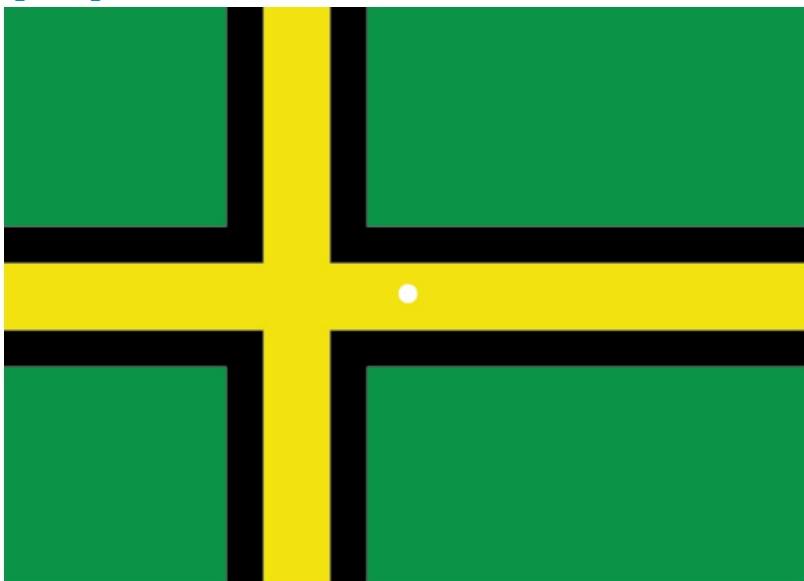
Color Vision

Normal-sighted individuals have three different types of cones that mediate color vision. Each of these cone types is maximally sensitive to a slightly different wavelength of light. According to the **trichromatic theory of color vision**, shown in [\[link\]](#), all colors in the spectrum can be produced by combining red, green, and blue. The three types of cones are each receptive to one of the colors.



The trichromatic theory of color vision is not the only theory—another major theory of color vision is known as the **opponent-process theory**. According to this theory, color is coded in opponent pairs: black-white, yellow-blue, and green-red. The basic idea is that some cells of the visual system are excited by one of the opponent colors and inhibited by the other. So, a cell that was excited by wavelengths associated with green would be inhibited by wavelengths associated with red, and vice versa. One of the implications of opponent processing is that we do not experience greenish-reds or yellowish-blues as colors. Another implication is that this leads to the experience of negative afterimages. An **afterimage** describes the

continuation of a visual sensation after removal of the stimulus. For example, when you stare briefly at the sun and then look away from it, you may still perceive a spot of light although the stimulus (the sun) has been removed. When color is involved in the stimulus, the color pairings identified in the opponent-process theory lead to a negative afterimage. You can test this concept using the flag in [\[link\]](#).



But these two theories—the trichromatic theory of color vision and the opponent-process theory—are not mutually exclusive. Research has shown that they just apply to different levels of the nervous system. For visual processing on the retina, trichromatic theory applies: the cones are responsive to three different wavelengths that represent red, blue, and green. But once the signal moves past the

retina on its way to the brain, the cells respond in a way consistent with opponent-process theory (Land, 1959; Kaiser, 1997).

Watch this [video](#) to learn about color vision in more detail.

Depth Perception

Our ability to perceive spatial relationships in three-dimensional (3-D) space is known as **depth perception**. With depth perception, we can describe things as being in front, behind, above, below, or to the side of other things.

Our world is three-dimensional, so it makes sense that our mental representation of the world has three-dimensional properties. We use a variety of cues in a visual scene to establish our sense of depth. Some of these are **binocular cues**, which means that they rely on the use of both eyes. One example of a binocular depth cue is **binocular disparity**, the slightly different view of the world that each of our eyes receives. To experience this slightly different view, do this simple exercise: extend your arm fully and extend one of your fingers and focus on that finger. Now, close your left

eye without moving your head, then open your left eye and close your right eye without moving your head. You will notice that your finger seems to shift as you alternate between the two eyes because of the slightly different view each eye has of your finger.

A 3-D movie works on the same principle: the special glasses you wear allow the two slightly different images projected onto the screen to be seen separately by your left and your right eye. As your brain processes these images, you have the illusion that the leaping animal or running person is coming right toward you.

Although we rely on binocular cues to experience depth in our 3-D world, we can also perceive depth in 2-D arrays. Think about all the paintings and photographs you have seen. Generally, you pick up on depth in these images even though the visual stimulus is 2-D. When we do this, we are relying on a number of **monocular cues**, or cues that require only one eye. If you think you can't see depth with one eye, note that you don't bump into things when using only one eye while walking—and, in fact, we have more monocular cues than binocular cues.

An example of a monocular cue would be what is known as linear perspective. **Linear perspective** refers to the fact that we perceive depth when we see two parallel lines that seem to converge in an

image ([\[link\]](#)). Some other monocular depth cues are interposition, the partial overlap of objects, and the relative size and closeness of images to the horizon.



Stereoblindness

Bruce Bridgeman was born with an extreme case of lazy eye that resulted in him being stereoblind, or unable to respond to binocular cues of depth. He relied heavily on monocular depth cues, but he never had a true appreciation of the 3-D nature of the world around him. This all changed one night in 2012 while Bruce was seeing a movie with his wife.

The movie the couple was going to see was shot in 3-D, and even though he thought it was a waste of money, Bruce paid for the 3-D glasses when he purchased his ticket. As soon as the film began, Bruce put on the glasses and experienced

something completely new. For the first time in his life he appreciated the true depth of the world around him. Remarkably, his ability to perceive depth persisted outside of the movie theater. There are cells in the nervous system that respond to binocular depth cues. Normally, these cells require activation during early development in order to persist, so experts familiar with Bruce's case (and others like his) assume that at some point in his development, Bruce must have experienced at least a fleeting moment of binocular vision. It was enough to ensure the survival of the cells in the visual system tuned to binocular cues. The mystery now is why it took Bruce nearly 70 years to have these cells activated (Peck, 2012).

Summary

Light waves cross the cornea and enter the eye at the pupil. The eye's lens focuses this light so that the image is focused on a region of the retina known as the fovea. The fovea contains cones that possess high levels of visual acuity and operate best in bright light conditions. Rods are located throughout the retina and operate best under dim light conditions. Visual information leaves the eye via the optic nerve. Information from each visual field is sent to the opposite side of the brain at the optic chiasm. Visual information then moves through a

number of brain sites before reaching the occipital lobe, where it is processed.

Two theories explain color perception. The trichromatic theory asserts that three distinct cone groups are tuned to slightly different wavelengths of light, and it is the combination of activity across these cone types that results in our perception of all the colors we see. The opponent-process theory of color vision asserts that color is processed in opponent pairs and accounts for the interesting phenomenon of a negative afterimage. We perceive depth through a combination of monocular and binocular depth cues.

Review Questions

The _____ is a small indentation of the retina that contains cones.

- A. optic chiasm
- B. optic nerve
- C. fovea
- D. iris

_____ operate best under bright light conditions.

- A. cones
 - B. rods
 - C. retinal ganglion cells
 - D. striate cortex
-

A

_____ depth cues require the use of both eyes.

- A. monocular
 - B. binocular
 - C. linear perspective
 - D. accommodating
-

B

If you were to stare at a green dot for a relatively long period of time and then shift your gaze to a blank white screen, you would see a _____ negative afterimage.

- A. blue
- B. yellow
- C. black
- D. red

Critical Thinking Question

Compare the two theories of color perception.
Are they completely different?

The trichromatic theory of color vision and the opponent-process theory are not mutually exclusive. Research has shown they apply to different levels of the nervous system. For visual processing on the retina, trichromatic theory applies: the cones are responsive to three different wavelengths that represent red, blue, and green. But once the signal moves past the retina on its way to the brain, the cells respond in a way consistent with opponent-process theory.

Color is not a physical property of our environment. What function (if any) do you think color vision serves?

Color vision probably serves multiple adaptive purposes. One popular hypothesis suggests that

seeing in color allowed our ancestors to differentiate ripened fruits and vegetables more easily.

Personal Application Question

Take a look at a few of your photos or personal works of art. Can you find examples of linear perspective as a potential depth cue?

Glossary

afterimage

continuation of a visual sensation after removal of the stimulus

binocular cue

cue that relies on the use of both eyes

binocular disparity

slightly different view of the world that each eye receives

blind spot

point where we cannot respond to visual information in that portion of the visual field

cone

specialized photoreceptor that works best in bright light conditions and detects color

cornea

transparent covering over the eye

depth perception

ability to perceive depth

fovea

small indentation in the retina that contains cones

iris

colored portion of the eye

lens

curved, transparent structure that provides additional focus for light entering the eye

linear perspective

perceive depth in an image when two parallel lines seem to converge

monocular cue

cue that requires only one eye

opponent-process theory of color perception

color is coded in opponent pairs: black-white, yellow-blue, and red-green

optic chiasm

X-shaped structure that sits just below the

brain's ventral surface; represents the merging of the optic nerves from the two eyes and the separation of information from the two sides of the visual field to the opposite side of the brain

optic nerve

carries visual information from the retina to the brain

photoreceptor

light-detecting cell

pupil

small opening in the eye through which light passes

retina

light-sensitive lining of the eye

rod

specialized photoreceptor that works well in low light conditions

trichromatic theory of color perception

color vision is mediated by the activity across the three groups of cones

Hearing and Vestibular Sensation

By the end of this section, you will be able to do the following:

- Describe the relationship of amplitude and frequency of a sound wave to attributes of sound
- Trace the path of sound through the auditory system to the site of transduction of sound
- Identify the structures of the vestibular system that respond to gravity

Audition, or hearing, is important to humans and to other animals for many different interactions. It enables an organism to detect and receive information about danger, such as an approaching predator, and to participate in communal exchanges like those concerning territories or mating. On the other hand, although it is physically linked to the auditory system, the vestibular system is not involved in hearing. Instead, an animal's vestibular system detects its own movement, both linear and angular acceleration and deceleration, and balance. For sound waves, wavelength corresponds to pitch. Amplitude of the wave corresponds to volume. The sound wave shown with a dashed line is softer in volume than the sound wave shown with a solid line. (credit: NIH)

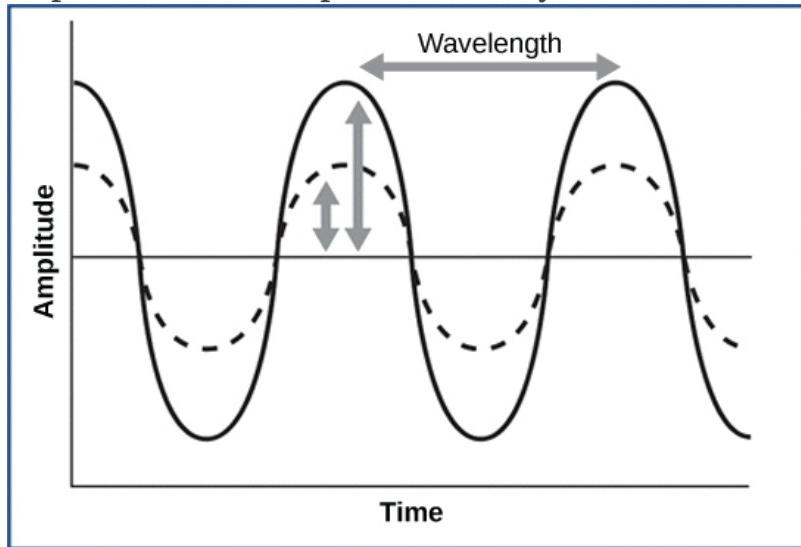
Sound

Auditory stimuli are sound waves, which are mechanical, pressure waves that move through a medium, such as air or water. There are no sound waves in a vacuum since there are no air molecules to move in waves. The speed of sound waves differs, based on altitude, temperature, and medium, but at sea level and a temperature of 20° C (68° F), sound waves travel in the air at about 343 meters per second.

As is true for all waves, there are four main characteristics of a sound wave: frequency, wavelength, period, and amplitude. Frequency is the number of waves per unit of time, and in sound is heard as pitch. High-frequency ($\geq 15.000\text{Hz}$) sounds are higher-pitched (short wavelength) than low-frequency (long wavelengths; $\leq 100\text{Hz}$) sounds. Frequency is measured in cycles per second, and for sound, the most commonly used unit is hertz (Hz), or cycles per second. Most humans can perceive sounds with frequencies between 30 and 20,000 Hz. Women are typically better at hearing high frequencies, but everyone's ability to hear high frequencies decreases with age. Dogs detect up to about 40,000 Hz; cats, 60,000 Hz; bats, 100,000 Hz; and dolphins 150,000 Hz, and American shad (*Alosa sapidissima*), a fish, can hear 180,000 Hz. Those frequencies above the human range are called ultrasound.

Amplitude, or the dimension of a wave from peak to

trough, in sound is heard as volume and is illustrated in [link]. The sound waves of louder sounds have greater amplitude than those of softer sounds. For sound, volume is measured in decibels (dB). The softest sound that a human can hear is the zero point. Humans speak normally at 60 decibels.

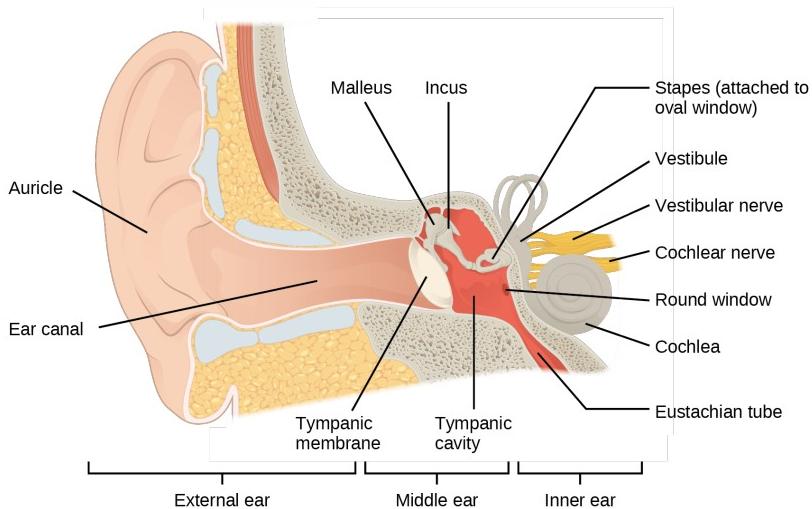


Sound travels through the outer ear to the middle ear, which is bounded on its exterior by the tympanic membrane. The middle ear contains three bones called ossicles that transfer the sound wave to the oval window, the exterior boundary of the inner ear. The organ of Corti, which is the organ of sound transduction, lies inside the cochlea.

Reception of Sound

In mammals, sound waves are collected by the external, cartilaginous part of the ear called the **pinna**, then travel through the auditory canal and

cause vibration of the thin diaphragm called the **tympanum** or ear drum, the innermost part of the **outer ear** (illustrated in [\[link\]](#)). Interior to the tympanum is the **middle ear**. The middle ear holds three small bones called the **ossicles**, which transfer energy from the moving tympanum to the inner ear. The three ossicles are the **malleus** (also known as the hammer), the **incus** (the anvil), and **stapes** (the stirrup). The aptly named stapes looks very much like a stirrup. The three ossicles are unique to mammals, and each plays a role in hearing. The malleus attaches at three points to the interior surface of the tympanic membrane. The incus attaches the malleus to the stapes. In humans, the stapes is not long enough to reach the tympanum. If we did not have the malleus and the incus, then the vibrations of the tympanum would never reach the inner ear. These bones also function to collect force and amplify sounds. The ear ossicles are homologous to bones in a fish mouth: the bones that support gills in fish are thought to be adapted for use in the vertebrate ear over evolutionary time. Many animals (frogs, reptiles, and birds, for example) use the stapes of the middle ear to transmit vibrations to the middle ear.



The hair cell is a mechanoreceptor with an array of stereocilia emerging from its apical surface. The stereocilia are tethered together by proteins that open ion channels when the array is bent toward the tallest member of their array, and closed when the array is bent toward the shortest member of their array.

Transduction of Sound

Vibrating objects, such as vocal cords, create sound waves or pressure waves in the air. When these pressure waves reach the ear, the ear transduces this mechanical stimulus (pressure wave) into a nerve impulse (electrical signal) that the brain perceives as sound. The pressure waves strike the tympanum, causing it to vibrate. The mechanical energy from the moving tympanum transmits the vibrations to the three bones of the middle ear. The stapes

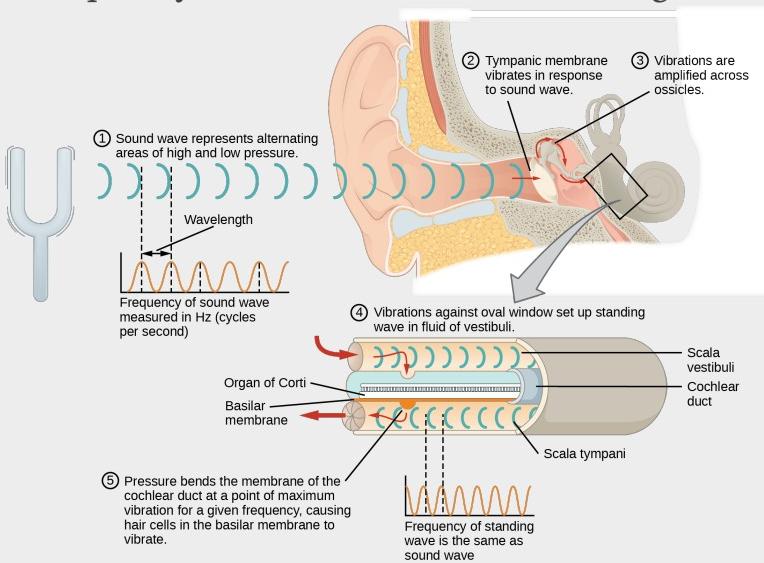
transmits the vibrations to a thin diaphragm called the **oval window**, which is the outermost structure of the **inner ear**. The structures of the inner ear are found in the **labyrinth**, a bony, hollow structure that is the most interior portion of the ear. Here, the energy from the sound wave is transferred from the stapes through the flexible oval window and to the fluid of the cochlea. The vibrations of the oval window create pressure waves in the fluid (perilymph) inside the cochlea. The **cochlea** is a whorled structure, like the shell of a snail, and it contains receptors for transduction of the mechanical wave into an electrical signal (as illustrated in [\[link\]](#)). Inside the cochlea, the **basilar membrane** is a mechanical analyzer that runs the length of the cochlea, curling toward the cochlea's center.

The mechanical properties of the basilar membrane change along its length, such that it is thicker, tauter, and narrower at the outside of the whorl (where the cochlea is largest), and thinner, floppier, and broader toward the apex, or center, of the whorl (where the cochlea is smallest). Different regions of the basilar membrane vibrate according to the frequency of the sound wave conducted through the fluid in the cochlea. For these reasons, the fluid-filled cochlea detects different wave frequencies (pitches) at different regions of the membrane. When the sound waves in the cochlear fluid contact the basilar membrane, it flexes back and forth in a

wave-like fashion. Above the basilar membrane is the **tectorial membrane**.

Visual Connection

A sound wave causes the tympanic membrane to vibrate. This vibration is amplified as it moves across the malleus, incus, and stapes. The amplified vibration is picked up by the oval window causing pressure waves in the fluid of the scala vestibuli and scala tympani. The complexity of the pressure waves is determined by the changes in amplitude and frequency of the sound waves entering the ear.



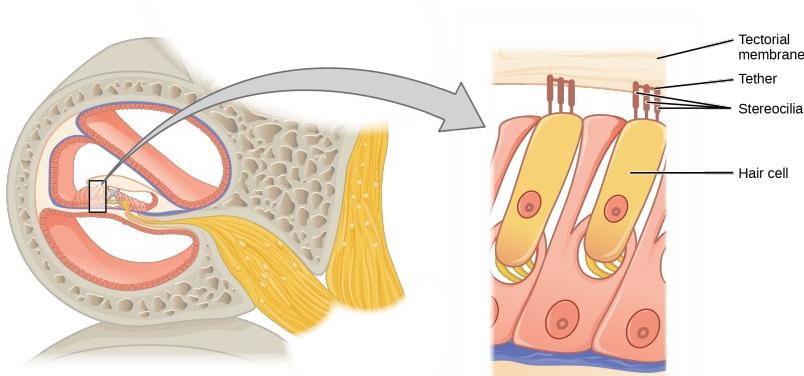
Cochlear implants can restore hearing in people who have a nonfunctional cochlea. The implant consists of a microphone that picks up sound. A speech processor selects sounds in the range of human speech, and a transmitter converts these

sounds to electrical impulses, which are then sent to the auditory nerve. Which of the following types of hearing loss would not be restored by a cochlear implant?

1. Hearing loss resulting from absence or loss of hair cells in the organ of Corti.
2. Hearing loss resulting from an abnormal auditory nerve.
3. Hearing loss resulting from fracture of the cochlea.
4. Hearing loss resulting from damage to bones of the middle ear.

The site of transduction is in the **organ of Corti** (spiral organ). It is composed of hair cells held in place above the basilar membrane like flowers projecting up from soil, with their exposed short, hair-like **stereocilia** contacting or embedded in the tectorial membrane above them. The inner hair cells are the primary auditory receptors and exist in a single row, numbering approximately 3,500. The stereocilia from inner hair cells extend into small dimples on the tectorial membrane's lower surface. The outer hair cells are arranged in three or four rows. They number approximately 12,000, and they function to fine tune incoming sound waves. The longer stereocilia that project from the outer hair cells actually attach to the tectorial membrane. All

of the stereocilia are mechanoreceptors, and when bent by vibrations they respond by opening a gated ion channel (refer to [\[link\]](#)). As a result, the hair cell membrane is depolarized, and a signal is transmitted to the cochlear nerve. Intensity (volume) of sound is determined by how many hair cells at a particular location are stimulated.



The hair cells are arranged on the basilar membrane in an orderly way. The basilar membrane vibrates in different regions, according to the frequency of the sound waves impinging on it. Likewise, the hair cells that lay above it are most sensitive to a specific frequency of sound waves. Hair cells can respond to a small range of similar frequencies, but they require stimulation of greater intensity to fire at frequencies outside of their optimal range. The difference in response frequency between adjacent inner hair cells is about 0.2 percent. Compare that

to adjacent piano strings, which are about six percent different. Place theory, which is the model for how biologists think pitch detection works in the human ear, states that high frequency sounds selectively vibrate the basilar membrane of the inner ear near the entrance port (the oval window). Lower frequencies travel farther along the membrane before causing appreciable excitation of the membrane. The basic pitch-determining mechanism is based on the location along the membrane where the hair cells are stimulated. The place theory is the first step toward an understanding of pitch perception. Considering the extreme pitch sensitivity of the human ear, it is thought that there must be some auditory “sharpening” mechanism to enhance the pitch resolution.

When sound waves produce fluid waves inside the cochlea, the basilar membrane flexes, bending the stereocilia that attach to the tectorial membrane. Their bending results in action potentials in the hair cells, and auditory information travels along the neural endings of the bipolar neurons of the hair cells (collectively, the auditory nerve) to the brain. When the hairs bend, they release an excitatory neurotransmitter at a synapse with a sensory neuron, which then conducts action potentials to the central nervous system. The cochlear branch of the vestibulocochlear cranial nerve sends information on hearing. The auditory system is very refined, and

there is some modulation or “sharpening” built in. The brain can send signals back to the cochlea, resulting in a change of length in the outer hair cells, sharpening or dampening the hair cells’ response to certain frequencies.

Link to Learning

Watch an [animation](#) of sound entering the outer ear, moving through the ear structure, stimulating cochlear nerve impulses, and eventually sending signals to the temporal lobe.

Higher Processing

The inner hair cells are most important for conveying auditory information to the brain. About 90 percent of the afferent neurons carry information from inner hair cells, with each hair cell synapsing with 10 or so neurons. Outer hair cells connect to only 10 percent of the afferent neurons, and each afferent neuron innervates many hair cells. The afferent, bipolar neurons that convey auditory information travel from the cochlea to the medulla, through the pons and midbrain in the brainstem, finally reaching the primary auditory cortex in the temporal lobe.

The structure of the vestibular labyrinth is shown.

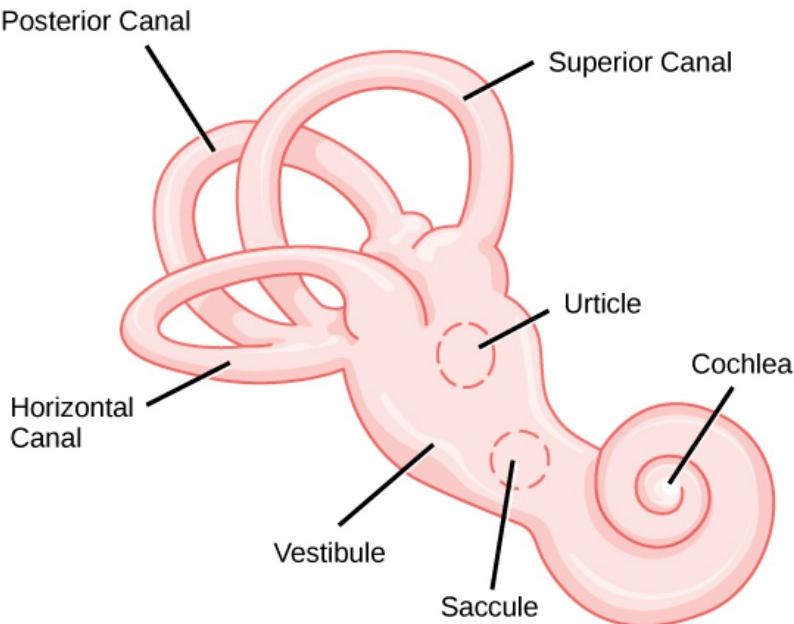
(credit: modification of work by NIH)

Vestibular Information

The stimuli associated with the vestibular system are linear acceleration (gravity) and angular acceleration and deceleration. Gravity, acceleration, and deceleration are detected by evaluating the inertia on receptive cells in the vestibular system. Gravity is detected through head position. Angular acceleration and deceleration are expressed through turning or tilting of the head.

The vestibular system has some similarities with the auditory system. It utilizes hair cells just like the auditory system, but it excites them in different ways. There are five vestibular receptor organs in the inner ear: the utricle, the saccule, and three semicircular canals. Together, they make up what's known as the vestibular labyrinth that is shown in [\[link\]](#). The utricle and saccule respond to acceleration in a straight line, such as gravity. The roughly 30,000 hair cells in the utricle and 16,000 hair cells in the saccule lie below a gelatinous layer, with their stereocilia projecting into the gelatin. Embedded in this gelatin are calcium carbonate crystals—like tiny rocks. When the head is tilted, the crystals continue to be pulled straight down by gravity, but the new angle of the head causes the gelatin to shift, thereby bending the stereocilia. The bending of the stereocilia stimulates the neurons,

and they signal to the brain that the head is tilted, allowing the maintenance of balance. It is the vestibular branch of the vestibulocochlear cranial nerve that deals with balance.



The fluid-filled **semicircular canals** are tubular loops set at oblique angles. They are arranged in three spatial planes. The base of each canal has a swelling that contains a cluster of hair cells. The hairs project into a gelatinous cap called the cupula and monitor angular acceleration and deceleration from rotation. They would be stimulated by driving your car around a corner, turning your head, or falling forward. One canal lies horizontally, while the other two lie at about 45 degree angles to the horizontal axis, as illustrated in [\[link\]](#). When the brain processes input from all three canals together,

it can detect angular acceleration or deceleration in three dimensions. When the head turns, the fluid in the canals shifts, thereby bending stereocilia and sending signals to the brain. Upon cessation accelerating or decelerating—or just moving—the movement of the fluid within the canals slows or stops. For example, imagine holding a glass of water. When moving forward, water may splash backwards onto the hand, and when motion has stopped, water may splash forward onto the fingers. While in motion, the water settles in the glass and does not splash. Note that the canals are not sensitive to velocity itself, but to changes in velocity, so moving forward at 60mph with your eyes closed would not give the sensation of movement, but suddenly accelerating or braking would stimulate the receptors.

Higher Processing

Hair cells from the utricle, saccule, and semicircular canals also communicate through bipolar neurons to the cochlear nucleus in the medulla. Cochlear neurons send descending projections to the spinal cord and ascending projections to the pons, thalamus, and cerebellum. Connections to the cerebellum are important for coordinated movements. There are also projections to the temporal cortex, which account for feelings of dizziness; projections to autonomic nervous system areas in the brainstem, which account for motion

sickness; and projections to the primary somatosensory cortex, which monitors subjective measurements of the external world and self-movement. People with lesions in the vestibular area of the somatosensory cortex see vertical objects in the world as being tilted. Finally, the vestibular signals project to certain optic muscles to coordinate eye and head movements.

Link to Learning

Click through this [interactive tutorial](#) to review the parts of the ear and how they function to process sound.

Section Summary

Audition is important for territory defense, predation, predator defense, and communal exchanges. The vestibular system, which is not auditory, detects linear acceleration and angular acceleration and deceleration. Both the auditory system and vestibular system use hair cells as their receptors.

Auditory stimuli are sound waves. The sound wave

energy reaches the outer ear (pinna, canal, tympanum), and vibrations of the tympanum send the energy to the middle ear. The middle ear bones shift and the stapes transfers mechanical energy to the oval window of the fluid-filled inner ear cochlea. Once in the cochlea, the energy causes the basilar membrane to flex, thereby bending the stereocilia on receptor hair cells. This activates the receptors, which send their auditory neural signals to the brain.

The vestibular system has five parts that work together to provide the sense of direction, thus helping to maintain balance. The utricle and saccule measure head orientation: their calcium carbonate crystals shift when the head is tilted, thereby activating hair cells. The semicircular canals work similarly, such that when the head is turned, the fluid in the canals bends stereocilia on hair cells. The vestibular hair cells also send signals to the thalamus and to the somatosensory cortex, but also to the cerebellum, the structure above the brainstem that plays a large role in timing and coordination of movement.

Visual Connection Questions

[link] Cochlear implants can restore hearing in

people who have a nonfunctional cochlea. The implant consists of a microphone that picks up sound. A speech processor selects sounds in the range of human speech, and a transmitter converts these sounds to electrical impulses, which are then sent to the auditory nerve. Which of the following types of hearing loss would not be restored by a cochlear implant?

1. Hearing loss resulting from absence or loss of hair cells in the organ of Corti.
2. Hearing loss resulting from an abnormal auditory nerve.
3. Hearing loss resulting from fracture of the cochlea.
4. Hearing loss resulting from damage to bones of the middle ear.

[\[link\]](#) B

Review Questions

In sound, pitch is measured in ___, and volume is measured in ___.

1. nanometers (nm); decibels (dB)
2. decibels (dB); nanometers (nm)

-
- 3. decibels (dB); hertz (Hz)
 - 4. hertz (Hz); decibels (dB)

D

Auditory hair cells are indirectly anchored to the ____.

- 1. basilar membrane
 - 2. oval window
 - 3. tectorial membrane
 - 4. ossicles
-

A

Which of the following are found both in the auditory system and the vestibular system?

- 1. basilar membrane
 - 2. hair cells
 - 3. semicircular canals
 - 4. ossicles
-

B

Benign Paroxysmal Positional Vertigo is a

disorder where some of the calcium carbonate crystals in the utricle migrate into the semicircular canals. Why does this condition cause periods of dizziness?

1. The hair cells in the semicircular canals will be constantly activated.
 2. The hair cells in the semicircular canals will now be stimulated by gravity.
 3. The utricle will no longer recognize acceleration.
 4. There will be too much volume in the semicircular canals for them to detect motion.
-

B

Critical Thinking Questions

How would a rise in altitude likely affect the speed of a sound transmitted through air? Why?

The sound would slow down, because it is transmitted through the particles (gas) and there are fewer particles (lower density) at higher altitudes.

How might being in a place with less gravity than Earth has (such as Earth's moon) affect vestibular sensation, and why?

Because vestibular sensation relies on gravity's effects on tiny crystals in the inner ear, a situation of reduced gravity would likely impair vestibular sensation.

How does the structure of the ear allow a person to determine where a sound originates?

The first step in processing a sound in humans is the collection of sound by the pinna. When a person encounters a sound, the pinna on both sides of the head will collect the vibrations. Since the waves originate from a single site, the two pinnae will not collect the sound at the exact same time. When the sound is processed by the auditory system, the brain is able to use this slight difference in timing to determine the location of the sound.

Glossary

audition

sense of hearing

basilar membrane

stiff structure in the cochlea that indirectly anchors auditory receptors

cochlea

whorled structure that contains receptors for transduction of the mechanical wave into an electrical signal

incus

(also, anvil) second of the three bones of the middle ear

inner ear

innermost part of the ear; consists of the cochlea and the vestibular system

labyrinth

bony, hollow structure that is the most internal part of the ear; contains the sites of transduction of auditory and vestibular information

malleus

(also, hammer) first of the three bones of the middle ear

middle ear

part of the hearing apparatus that functions to transfer energy from the tympanum to the oval window of the inner ear

organ of Corti

in the basilar membrane, the site of the transduction of sound, a mechanical wave, to a neural signal

ossicle

one of the three bones of the middle ear

outer ear

part of the ear that consists of the pinna, ear canal, and tympanum and which conducts sound waves into the middle ear

oval window

thin diaphragm between the middle and inner ears that receives sound waves from contact with the stapes bone of the middle ear

pinna

cartilaginous outer ear

semicircular canal

one of three half-circular, fluid-filled tubes in the vestibular labyrinth that monitors angular acceleration and deceleration

stapes

(also, stirrup) third of the three bones of the middle ear

stereocilia

in the auditory system, hair-like projections

from hair cells that help detect sound waves

tectorial membrane

cochlear structure that lies above the hair cells and participates in the transduction of sound at the hair cells

tympanum

(also, tympanic membrane or ear drum) thin diaphragm between the outer and middle ears

ultrasound

sound frequencies above the human detectable ceiling of approximately 20,000 Hz

Taste and Smell

By the end of this section, you will be able to:

- Explain in what way smell and taste stimuli differ from other sensory stimuli
- Identify the five primary tastes that can be distinguished by humans
- Explain in anatomical terms why a dog's sense of smell is more acute than a human's

Taste, also called **gustation**, and smell, also called **olfaction**, are the most interconnected senses in that both involve molecules of the stimulus entering the body and bonding to receptors. Smell lets an animal sense the presence of food or other animals—whether potential mates, predators, or prey—or other chemicals in the environment that can impact their survival. Similarly, the sense of taste allows animals to discriminate between types of foods. While the value of a sense of smell is obvious, what is the value of a sense of taste? Different tasting foods have different attributes, both helpful and harmful. For example, sweet-tasting substances tend to be highly caloric, which could be necessary for survival in lean times. Bitterness is associated with toxicity, and sourness is associated with spoiled food. Salty foods are valuable in maintaining homeostasis by helping the body retain water and by providing ions necessary for cells to function.

Tastes and Odors

Both taste and odor stimuli are molecules taken in from the environment. The primary tastes detected by humans are sweet, sour, bitter, salty and umami. The first four tastes need little explanation. The identification of **umami** as a fundamental taste occurred fairly recently—it was identified in 1908 by Japanese scientist Kikunae Ikeda while he worked with seaweed broth, but it was not widely accepted as a taste that could be physiologically distinguished until many years later. The taste of umami, also known as savoriness, is attributable to the taste of the amino acid L-glutamate. In fact, monosodium glutamate, or MSG, is often used in cooking to enhance the savory taste of certain foods. What is the adaptive value of being able to distinguish umami? Savory substances tend to be high in protein.

All odors that we perceive are molecules in the air we breathe. If a substance does not release molecules into the air from its surface, it has no smell. And if a human or other animal does not have a receptor that recognizes a specific molecule, then that molecule has no smell. Humans have about 350 olfactory receptor subtypes that work in various combinations to allow us to sense about 10,000 different odors. Compare that to mice, for example, which have about 1,300 olfactory receptor types, and therefore probably sense more odors. Both

odors and tastes involve molecules that stimulate specific chemoreceptors. Although humans commonly distinguish taste as one sense and smell as another, they work together to create the perception of flavor. A person's perception of flavor is reduced if he or she has congested nasal passages. In the human olfactory system, (a) bipolar olfactory neurons extend from (b) the olfactory epithelium, where olfactory receptors are located, to the olfactory bulb. (credit: modification of work by Patrick J. Lynch, medical illustrator; C. Carl Jaffe, MD, cardiologist)(a) Foliate, circumvallate, and fungiform papillae are located on different regions of the tongue. (b) Foliate papillae are prominent protrusions on this light micrograph. (credit a: modification of work by NCI; scale-bar data from Matt Russell) Pores in the tongue allow tastants to enter taste pores in the tongue. (credit: modification of work by Vincenzo Rizzo)

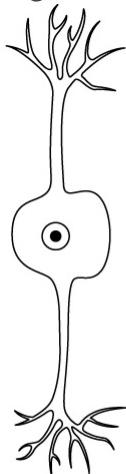
Reception and Transduction

Odorants (odor molecules) enter the nose and dissolve in the olfactory epithelium, the mucosa at the back of the nasal cavity (as illustrated in [\[link\]](#)). The **olfactory epithelium** is a collection of specialized olfactory receptors in the back of the nasal cavity that spans an area about 5 cm^2 in humans. Recall that sensory cells are neurons. An **olfactory receptor**, which is a dendrite of a specialized neuron, responds when it binds certain

molecules inhaled from the environment by sending impulses directly to the olfactory bulb of the brain. Humans have about 12 million olfactory receptors, distributed among hundreds of different receptor types that respond to different odors. Twelve million seems like a large number of receptors, but compare that to other animals: rabbits have about 100 million, most dogs have about 1 billion, and bloodhounds—dogs selectively bred for their sense of smell—have about 4 billion. The overall size of the olfactory epithelium also differs between species, with that of bloodhounds, for example, being many times larger than that of humans.

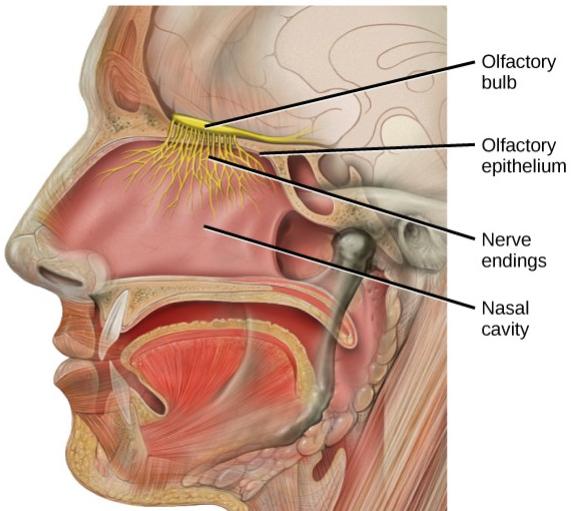
Olfactory neurons are **bipolar neurons** (neurons with two processes from the cell body). Each neuron has a single dendrite buried in the olfactory epithelium, and extending from this dendrite are 5 to 20 receptor-laden, hair-like cilia that trap odorant molecules. The sensory receptors on the cilia are proteins, and it is the variations in their amino acid chains that make the receptors sensitive to different odorants. Each olfactory sensory neuron has only one type of receptor on its cilia, and the receptors are specialized to detect specific odorants, so the bipolar neurons themselves are specialized. When an odorant binds with a receptor that recognizes it, the sensory neuron associated with the receptor is stimulated. Olfactory stimulation is the only sensory information that directly reaches the cerebral cortex, whereas other sensations are relayed

through the thalamus.



Bipolar neuron

(a)



(b)

Evolution Connection

Pheromones

A **pheromone** is a chemical released by an animal that affects the behavior or physiology of animals of the same species. Pheromonal signals can have profound effects on animals that inhale them, but pheromones apparently are not consciously perceived in the same way as other odors. There are several different types of pheromones, which are released in urine or as glandular secretions. Certain pheromones are attractants to potential mates, others are repellants to potential competitors of the same sex, and still others play roles in mother-infant attachment. Some pheromones can also influence the timing of

puberty, modify reproductive cycles, and even prevent embryonic implantation. While the roles of pheromones in many nonhuman species are important, pheromones have become less important in human behavior over evolutionary time compared to their importance to organisms with more limited behavioral repertoires.

The vomeronasal organ (VNO, or Jacobson's organ) is a tubular, fluid-filled, olfactory organ present in many vertebrate animals that sits adjacent to the nasal cavity. It is very sensitive to pheromones and is connected to the nasal cavity by a duct. When molecules dissolve in the mucosa of the nasal cavity, they then enter the VNO where the pheromone molecules among them bind with specialized pheromone receptors. Upon exposure to pheromones from their own species or others, many animals, including cats, may display the flehmen response (shown in [\[link\]](#)), a curling of the upper lip that helps pheromone molecules enter the VNO.

Pheromonal signals are sent, not to the main olfactory bulb, but to a different neural structure that projects directly to the amygdala (recall that the amygdala is a brain center important in emotional reactions, such as fear). The pheromonal signal then continues to areas of the hypothalamus that are key to reproductive physiology and behavior. While some scientists assert that the VNO is apparently functionally vestigial in humans, even though there is a similar structure located near

human nasal cavities, others are researching it as a possible functional system that may, for example, contribute to synchronization of menstrual cycles in women living in close proximity.

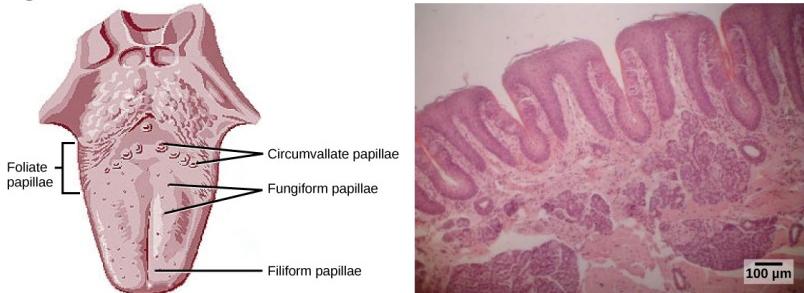
The flehmen response in this tiger results in the curling of the upper lip and helps airborne pheromone molecules enter the vomeronasal organ. (credit: modification of work by "chadh"/Flickr)



Taste

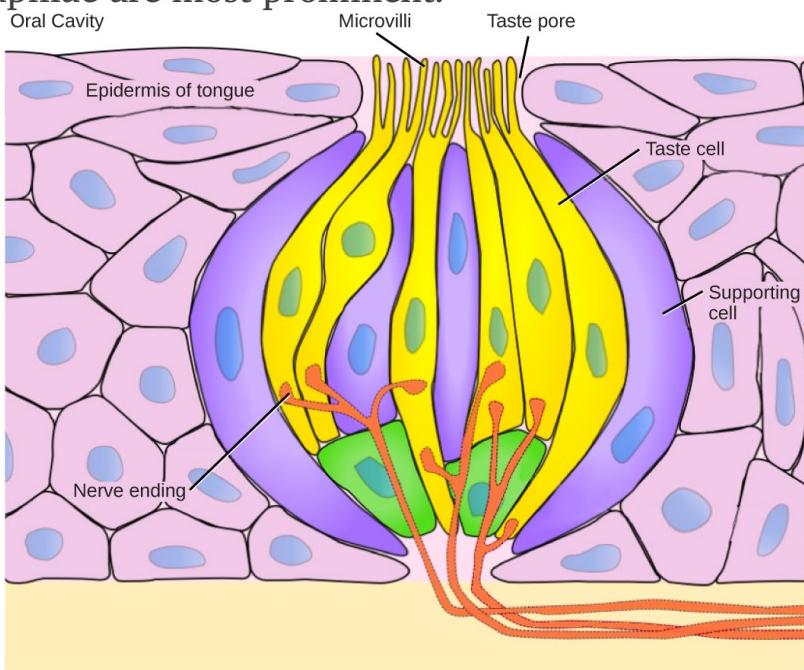
Detecting a taste (gustation) is fairly similar to detecting an odor (olfaction), given that both taste and smell rely on chemical receptors being stimulated by certain molecules. The primary organ of taste is the taste bud. A **taste bud** is a cluster of gustatory receptors (taste cells) that are located

within the bumps on the tongue called **papillae** (singular: papilla) (illustrated in [\[link\]](#)). There are several structurally distinct papillae. Filiform papillae, which are located across the tongue, are tactile, providing friction that helps the tongue move substances, and contain no taste cells. In contrast, fungiform papillae, which are located mainly on the anterior two-thirds of the tongue, each contain one to eight taste buds and also have receptors for pressure and temperature. The large circumvallate papillae contain up to 100 taste buds and form a V near the posterior margin of the tongue.



In addition to those two types of chemically and mechanically sensitive papillae are foliate papillae—leaf-like papillae located in parallel folds along the edges and toward the back of the tongue, as seen in the [\[link\]](#) micrograph. Foliate papillae contain about 1,300 taste buds within their folds. Finally, there are circumvallate papillae, which are wall-like papillae in the shape of an inverted “V” at the back of the tongue. Each of these papillae is surrounded by a groove and contains about 250 taste buds.

Each taste bud's taste cells are replaced every 10 to 14 days. These are elongated cells with hair-like processes called microvilli at the tips that extend into the taste bud pore (illustrate in [\[link\]](#)). Food molecules (**tastants**) are dissolved in saliva, and they bind with and stimulate the receptors on the microvilli. The receptors for tastants are located across the outer portion and front of the tongue, outside of the middle area where the filiform papillae are most prominent.



In humans, there are five primary tastes, and each taste has only one corresponding type of receptor. Thus, like olfaction, each receptor is specific to its stimulus (tastant). Transduction of the five tastes happens through different mechanisms that reflect the molecular composition of the tastant. A salty

tastant (containing NaCl) provides the sodium ions (Na^+) that enter the taste neurons and excite them directly. Sour tastants are acids and belong to the thermoreceptor protein family. Binding of an acid or other sour-tasting molecule triggers a change in the ion channel and these increase hydrogen ion (H^+) concentrations in the taste neurons, thus depolarizing them. Sweet, bitter, and umami tastants require a G-protein coupled receptor. These tastants bind to their respective receptors, thereby exciting the specialized neurons associated with them.

Both tasting abilities and sense of smell change with age. In humans, the senses decline dramatically by age 50 and continue to decline. A child may find a food to be too spicy, whereas an elderly person may find the same food to be bland and unappetizing.

Link to Learning



View this [animation](#) that shows how the sense of taste works.

Smell and Taste in the Brain

Olfactory neurons project from the olfactory epithelium to the olfactory bulb as thin, unmyelinated axons. The **olfactory bulb** is composed of neural clusters called **glomeruli**, and each glomerulus receives signals from one type of olfactory receptor, so each glomerulus is specific to one odorant. From glomeruli, olfactory signals travel directly to the olfactory cortex and then to the frontal cortex and the thalamus. Recall that this is a different path from most other sensory information, which is sent directly to the thalamus before ending up in the cortex. Olfactory signals also travel directly to the amygdala, thereafter reaching the hypothalamus, thalamus, and frontal cortex. The last structure that olfactory signals directly travel to is a cortical center in the temporal lobe structure important in spatial, autobiographical, declarative, and episodic memories. Olfaction is finally processed by areas of the brain that deal with memory, emotions, reproduction, and thought.

Taste neurons project from taste cells in the tongue, esophagus, and palate to the medulla, in the brainstem. From the medulla, taste signals travel to the thalamus and then to the primary gustatory cortex. Information from different regions of the

tongue is segregated in the medulla, thalamus, and cortex.

Section Summary

There are five primary tastes in humans: sweet, sour, bitter, salty, and umami. Each taste has its own receptor type that responds only to that taste. Tastants enter the body and are dissolved in saliva. Taste cells are located within taste buds, which are found on three of the four types of papillae in the mouth.

Regarding olfaction, there are many thousands of odorants, but humans detect only about 10,000. Like taste receptors, olfactory receptors are each responsive to only one odorant. Odorants dissolve in nasal mucosa, where they excite their corresponding olfactory sensory cells. When these cells detect an odorant, they send their signals to the main olfactory bulb and then to other locations in the brain, including the olfactory cortex.

Review Questions

Which of the following has the fewest taste receptors?

-
1. fungiform papillae
 2. circumvallate papillae
 3. foliate papillae
 4. filiform papillae

D

How many different taste molecules do taste cells each detect?

1. one
 2. five
 3. ten
 4. It depends on the spot on the tongue
-

A

Salty foods activate the taste cells by ____.

1. exciting the taste cell directly
 2. causing hydrogen ions to enter the cell
 3. causing sodium channels to close
 4. binding directly to the receptors
-

A

All sensory signals except ____ travel to the ____ in the brain before the cerebral cortex.

1. vision; thalamus
 2. olfaction; thalamus
 3. vision; cranial nerves
 4. olfaction; cranial nerves
-

B

Free Response

From the perspective of the recipient of the signal, in what ways do pheromones differ from other odorants?

Pheromones may not be consciously perceived, and pheromones can have direct physiological and behavioral effects on their recipients.

What might be the effect on an animal of not being able to perceive taste?

The animal might not be able to recognize the differences in food sources and thus might not

be able to discriminate between spoiled food and safe food or between foods that contain necessary nutrients, such as proteins, and foods that do not.

Glossary

bipolar neuron

neuron with two processes from the cell body, typically in opposite directions

glomerulus

in the olfactory bulb, one of the two neural clusters that receives signals from one type of olfactory receptor

gustation

sense of taste

odorant

airborne molecule that stimulates an olfactory receptor

olfaction

sense of smell

olfactory bulb

neural structure in the vertebrate brain that receives signals from olfactory receptors

olfactory epithelium

specialized tissue in the nasal cavity where olfactory receptors are located

olfactory receptor

dendrite of a specialized neuron

papilla

one of the small bump-like projections from the tongue

pheromone

substance released by an animal that can affect the physiology or behavior of other animals

tastant

food molecule that stimulates gustatory receptors

taste bud

clusters of taste cells

umami

one of the five basic tastes, which is described as “savory” and which may be largely the taste of L-glutamate

Types of Skeletal Systems

By the end of this section, you will be able to do the following:

- Discuss the different types of skeletal systems
- Explain the role of the human skeletal system
- Compare and contrast different skeletal systems

A skeletal system is necessary to support the body, protect internal organs, and allow for the movement of an organism. There are three different skeleton designs that fulfill these functions: hydrostatic skeleton, exoskeleton, and endoskeleton.

The skeleton of the red-knobbed sea star (*Protoreaster linckii*) is an example of a hydrostatic skeleton. (credit: “Amada44”/Wikimedia Commons)

Hydrostatic Skeleton

A **hydrostatic skeleton** is a skeleton formed by a fluid-filled compartment within the body, called the coelom. The organs of the coelom are supported by the aqueous fluid, which also resists external compression. This compartment is under hydrostatic pressure because of the fluid and supports the other organs of the organism. This type of skeletal system is found in soft-bodied animals such as sea anemones, earthworms, Cnidaria, and other invertebrates ([\[link\]](#)).



Movement in a hydrostatic skeleton is provided by muscles that surround the coelom. The muscles in a hydrostatic skeleton contract to change the shape of the coelom; the pressure of the fluid in the coelom produces movement. For example, earthworms move by waves of muscular contractions of the skeletal muscle of the body wall hydrostatic skeleton, called peristalsis, which alternately shorten and lengthen the body. Lengthening the body extends the anterior end of the organism. Most organisms have a mechanism to fix themselves in the substrate. Shortening the muscles then draws the posterior portion of the body forward. Although a hydrostatic skeleton is well-suited to invertebrate organisms such as earthworms and some aquatic organisms, it is not an efficient skeleton for terrestrial animals.

Muscles attached to the exoskeleton of the Halloween crab (*Gecarcinus quadratus*) allow it to

move.

Exoskeleton

An **exoskeleton** is an external skeleton that consists of a hard encasement on the surface of an organism. For example, the shells of crabs and insects are exoskeletons ([\[link\]](#)). This skeleton type provides defence against predators, supports the body, and allows for movement through the contraction of attached muscles. As with vertebrates, muscles must cross a joint inside the exoskeleton. Shortening of the muscle changes the relationship of the two segments of the exoskeleton. Arthropods such as crabs and lobsters have exoskeletons that consist of 30–50 percent chitin, a polysaccharide derivative of glucose that is a strong but flexible material. Chitin is secreted by the epidermal cells. The exoskeleton is further strengthened by the addition of calcium carbonate in organisms such as the lobster. Because the exoskeleton is acellular, arthropods must periodically shed their exoskeletons because the exoskeleton does not grow as the organism grows.



The skeletons of humans and horses are examples of endoskeletons. (credit: Ross Murphy)

Endoskeleton

An **endoskeleton** is a skeleton that consists of hard, mineralized structures located within the soft tissue of organisms. An example of a primitive endoskeletal structure is the spicules of sponges. The bones of vertebrates are composed of tissues, whereas sponges have no true tissues ([\[link\]](#)). Endoskeletons provide support for the body, protect internal organs, and allow for movement through contraction of muscles attached to the skeleton.



The human skeleton is an endoskeleton that consists of 206 bones in the adult. It has five main functions: providing support to the body, storing minerals and lipids, producing blood cells, protecting internal organs, and allowing for movement. The skeletal system in vertebrates is divided into the axial skeleton (which consists of the skull, vertebral column, and rib cage), and the appendicular

skeleton (which consists of the shoulders, limb bones, the pectoral girdle, and the pelvic girdle).

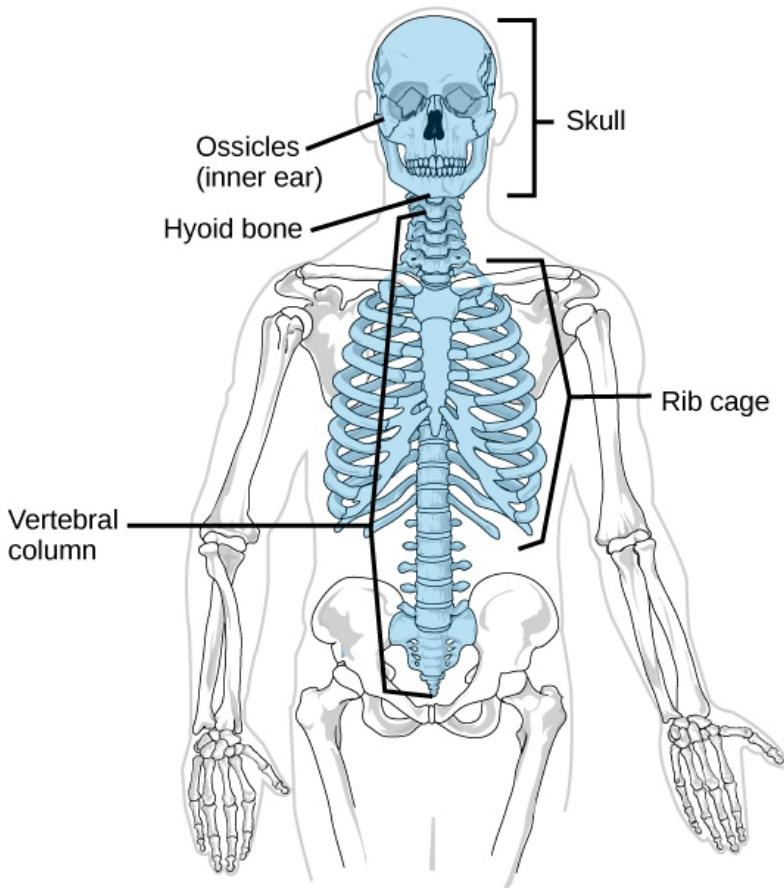
Link to Learning

Visit the [interactive body](#) site to build a virtual skeleton: select "skeleton" and click through the activity to place each bone.

The axial skeleton consists of the bones of the skull, ossicles of the middle ear, hyoid bone, vertebral column, and rib cage. (credit: modification of work by Mariana Ruiz Villareal)

Human Axial Skeleton

The **axial skeleton** forms the central axis of the body and includes the bones of the skull, ossicles of the middle ear, hyoid bone of the throat, vertebral column, and the thoracic cage (ribcage) ([\[link\]](#)). The function of the axial skeleton is to provide support and protection for the brain, the spinal cord, and the organs in the ventral body cavity. It provides a surface for the attachment of muscles that move the head, neck, and trunk, performs respiratory movements, and stabilizes parts of the appendicular skeleton.

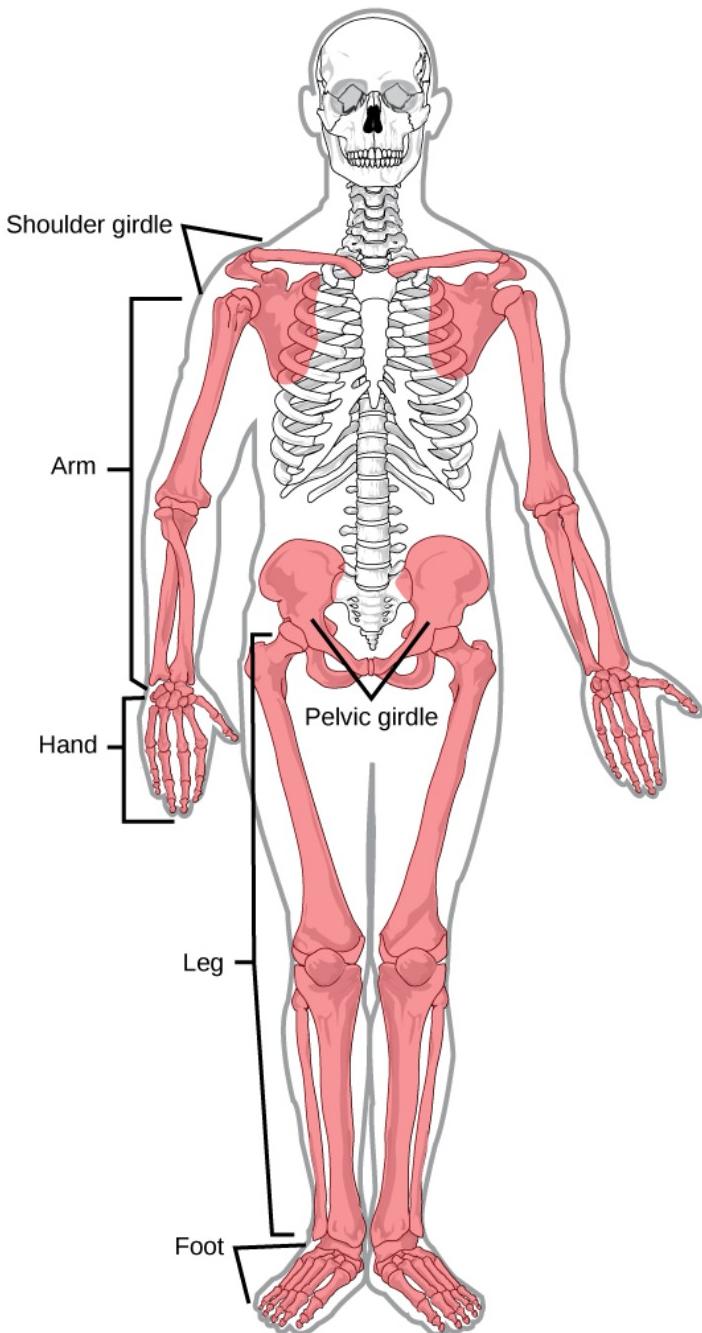


The appendicular skeleton is composed of the bones of the pectoral limbs (arm, forearm, hand), the pelvic limbs (thigh, leg, foot), the pectoral girdle, and the pelvic girdle. (credit: modification of work by Mariana Ruiz Villareal)

Human Appendicular Skeleton

The **appendicular skeleton** is composed of the bones of the upper limbs (which function to grasp

and manipulate objects) and the lower limbs (which permit locomotion). It also includes the pectoral girdle, or shoulder girdle, that attaches the upper limbs to the body, and the pelvic girdle that attaches the lower limbs to the body ([\[link\]](#)).



Section Summary

The three types of skeleton designs are hydrostatic skeletons, exoskeletons, and endoskeletons. A hydrostatic skeleton is formed by a fluid-filled compartment held under hydrostatic pressure; movement is created by the muscles producing pressure on the fluid. An exoskeleton is a hard external skeleton that protects the outer surface of an organism and enables movement through muscles attached on the inside. An endoskeleton is an internal skeleton composed of hard, mineralized tissue that also enables movement by attachment to muscles. The human skeleton is an endoskeleton that is composed of the axial and appendicular skeleton. The axial skeleton is composed of the bones of the skull, ossicles of the ear, hyoid bone, vertebral column, and ribcage. The skull consists of eight cranial bones and 14 facial bones. Six bones make up the ossicles of the middle ear, while the hyoid bone is located in the neck under the mandible. The vertebral column contains 26 bones, and it surrounds and protects the spinal cord. The thoracic cage consists of the sternum, ribs, thoracic vertebrae, and costal cartilages. The appendicular skeleton is made up of the limbs of the upper and lower limbs. The pectoral girdle is composed of the clavicles and the scapulae. The upper limb contains 30 bones in the arm, the forearm, and the hand. The pelvic girdle attaches the lower limbs to the axial skeleton. The lower limb includes the bones of the

thigh, the leg, and the foot.

Glossary

appendicular skeleton

composed of the bones of the upper limbs, which function to grasp and manipulate objects, and the lower limbs, which permit locomotion

articulation

any place where two bones are joined

auditory ossicle

(also, middle ear) transduces sounds from the air into vibrations in the fluid-filled cochlea

axial skeleton

forms the central axis of the body and includes the bones of the skull, the ossicles of the middle ear, the hyoid bone of the throat, the vertebral column, and the thoracic cage (ribcage)

carpus

eight bones that comprise the wrist

clavicle

S-shaped bone that positions the arms laterally

coxal bone

hip bone

cranial bone

one of eight bones that form the cranial cavity that encloses the brain and serves as an attachment site for the muscles of the head and neck

endoskeleton

skeleton of living cells that produces a hard, mineralized tissue located within the soft tissue of organisms

exoskeleton

a secreted cellular product external skeleton that consists of a hard encasement on the surface of an organism

facial bone

one of the 14 bones that form the face; provides cavities for the sense organs (eyes, mouth, and nose) and attachment points for facial muscles

femur

(also, thighbone) longest, heaviest, and strongest bone in the body

fibula

(also, calf bone) parallels and articulates with the tibia

forearm

extends from the elbow to the wrist and
consists of two bones: the ulna and the radius

humerus

only bone of the arm

hydrostatic skeleton

skeleton that consists of aqueous fluid held
under pressure in a closed body compartment

hyoid bone

lies below the mandible in the front of the
neck

intervertebral disc

composed of fibrous cartilage; lies between
adjacent vertebrae from the second cervical
vertebra to the sacrum

lower limb

consists of the thigh, the leg, and the foot

metacarpus

five bones that comprise the palm

metatarsal

one of the five bones of the foot

patella

(also, kneecap) triangular bone that lies
anterior to the knee joint

pectoral girdle

bones that transmit the force generated by the upper limbs to the axial skeleton

phalange

one of the bones of the fingers or toes

pelvic girdle

bones that transmit the force generated by the lower limbs to the axial skeleton

radius

bone located along the lateral (thumb) side of the forearm; articulates with the humerus at the elbow

rib

one of 12 pairs of long, curved bones that attach to the thoracic vertebrae and curve toward the front of the body to form the ribcage

scapula

flat, triangular bone located at the posterior pectoral girdle

skull

bone that supports the structures of the face and protects the brain

sternum

(also, breastbone) long, flat bone located at

the front of the chest

tarsal

one of the seven bones of the ankle

thoracic cage

(also, ribcage) skeleton of the chest, which consists of the ribs, thoracic vertebrae, sternum, and costal cartilages

tibia

(also, shinbone) large bone of the leg that is located directly below the knee

ulna

bone located on the medial aspect (pinky-finger side) of the forearm

vertebral column

(also, spine) surrounds and protects the spinal cord, supports the head, and acts as an attachment point for ribs and muscles of the back and neck

Bone

By the end of this section, you will be able to do the following:

- Classify the different types of bones in the skeleton
- Explain the role of the different cell types in bone
- Explain how bone forms during development

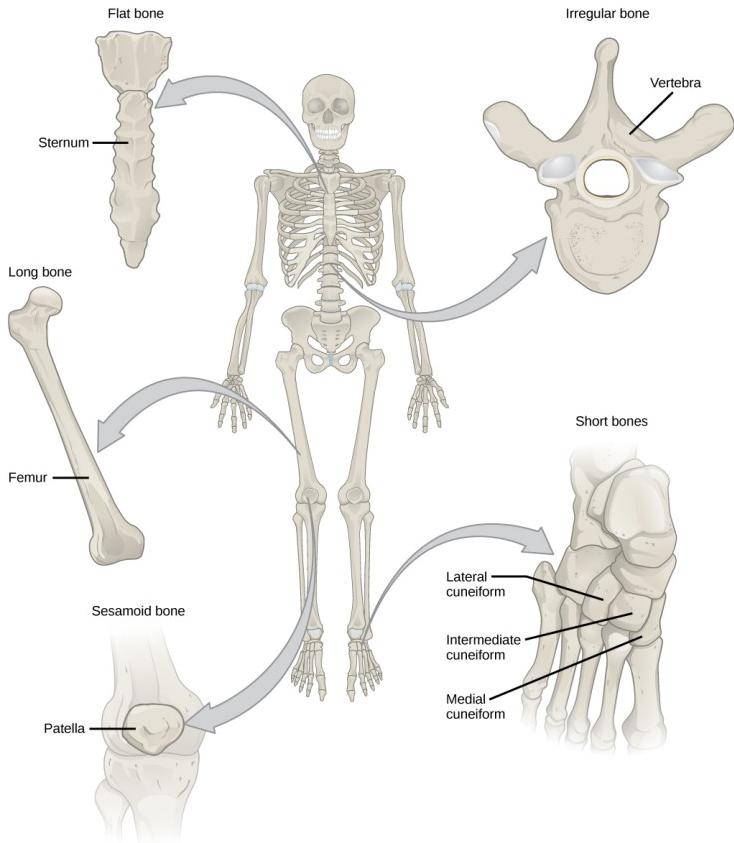
Bone, or osseous tissue, is a connective tissue that constitutes the endoskeleton. It contains specialized cells and a matrix of mineral salts and collagen fibers.

The mineral salts primarily include hydroxyapatite, a mineral formed from calcium phosphate.

Calcification is the process of deposition of mineral salts on the collagen fiber matrix that crystallizes and hardens the tissue. The process of calcification only occurs in the presence of collagen fibers.

The bones of the human skeleton are classified by their shape: long bones, short bones, flat bones, sutural bones, sesamoid bones, and irregular bones ([\[link\]](#)).

Shown are different types of bones: flat, irregular, long, short, and sesamoid.

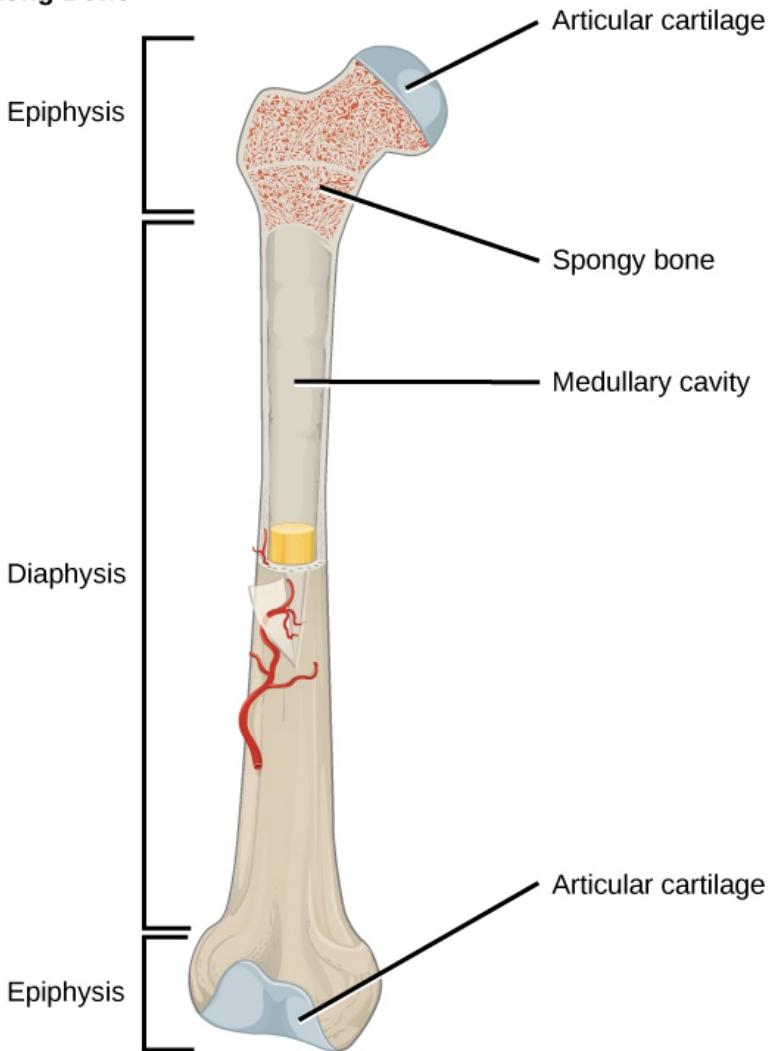


Long bones are longer than they are wide and have a shaft and two ends. The **diaphysis**, or central shaft, contains bone marrow in a marrow cavity. The rounded ends, the **epiphyses**, are covered with articular cartilage and are filled with red bone marrow, which produces blood cells ([\[link\]](#)). Most of the limb bones are long bones—for example, the femur, tibia, ulna, and radius. Exceptions to this include the patella and the bones of the wrist and ankle.

The long bone is covered by articular cartilage at

either end and contains bone marrow (shown in yellow in this illustration) in the marrow cavity.

Long Bone



Short bones, or cuboidal bones, are bones that are the same width and length, giving them a cube-like shape. For example, the bones of the wrist (carpals) and ankle (tarsals) are short bones ([\[link\]](#)).

Flat bones are thin and relatively broad bones that are found where extensive protection of organs is required or where broad surfaces of muscle attachment are required. Examples of flat bones are the sternum (breast bone), ribs, scapulae (shoulder blades), and the roof of the skull ([\[link\]](#)).

Irregular bones are bones with complex shapes. These bones may have short, flat, notched, or ridged surfaces. Examples of irregular bones are the vertebrae, hip bones, and several skull bones.

Sesamoid bones are small, flat bones and are shaped similarly to a sesame seed. The patellae are sesamoid bones ([\[link\]](#)). Sesamoid bones develop inside tendons and may be found near joints at the knees, hands, and feet.

The patella of the knee is an example of a sesamoid bone.



Sutural bones are small, flat, irregularly shaped bones. They may be found between the flat bones of the skull. They vary in number, shape, size, and position.

Trabeculae in spongy bone are arranged such that one side of the bone bears tension and the other withstands compression.

Bone Tissue

Bones are considered organs because they contain various types of tissue, such as blood, connective tissue, nerves, and bone tissue. Osteocytes, the living cells of bone tissue, form the mineral matrix of bones. There are two types of bone tissue:

compact and spongy.

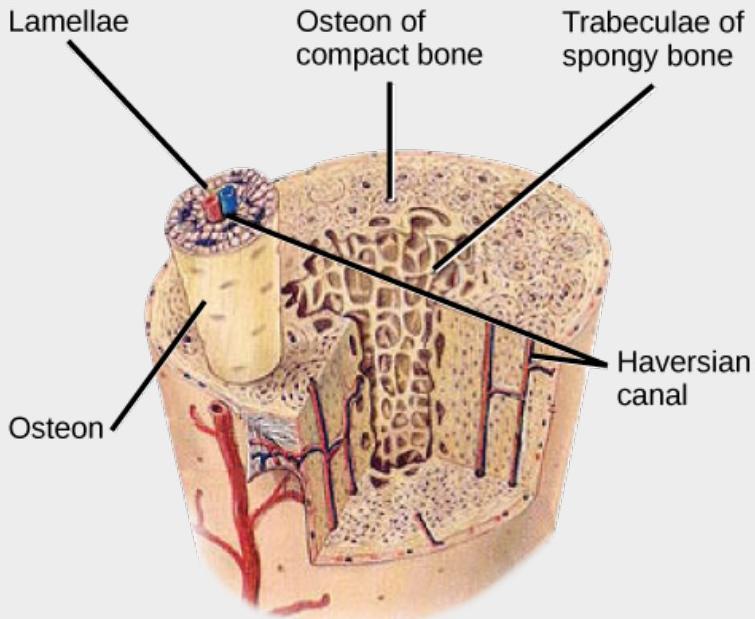
Compact Bone Tissue

Compact bone (or cortical bone) forms the hard external layer of all bones and surrounds the medullary cavity, or bone marrow. It provides protection and strength to bones. Compact bone tissue consists of units called osteons or Haversian systems. **Osteons** are cylindrical structures that contain a mineral matrix and living osteocytes connected by canaliculi, which transport blood. They are aligned parallel to the long axis of the bone. Each osteon consists of **lamellae**, which are layers of compact matrix that surround a central canal called the Haversian canal. The **Haversian canal** (osteonic canal) contains the bone's blood vessels and nerve fibers ([\[link\]](#)). Osteons in compact bone tissue are aligned in the same direction along lines of stress and help the bone resist bending or fracturing. Therefore, compact bone tissue is prominent in areas of bone at which stresses are applied in only a few directions.

Visual Connection

Compact bone tissue consists of osteons that are aligned parallel to the long axis of the bone, and the Haversian canal that contains the bone's blood vessels and nerve fibers. The inner layer of bones

consists of spongy bone tissue. The small dark ovals in the osteon represent the living osteocytes.
(credit: modification of work by NCI, NIH)



Which of the following statements about bone tissue is false?

1. Compact bone tissue is made of cylindrical osteons that are aligned such that they travel the length of the bone.
2. Haversian canals contain blood vessels only.
3. Haversian canals contain blood vessels and nerve fibers.
4. Spongy tissue is found on the interior of the bone, and compact bone tissue is found on the exterior.

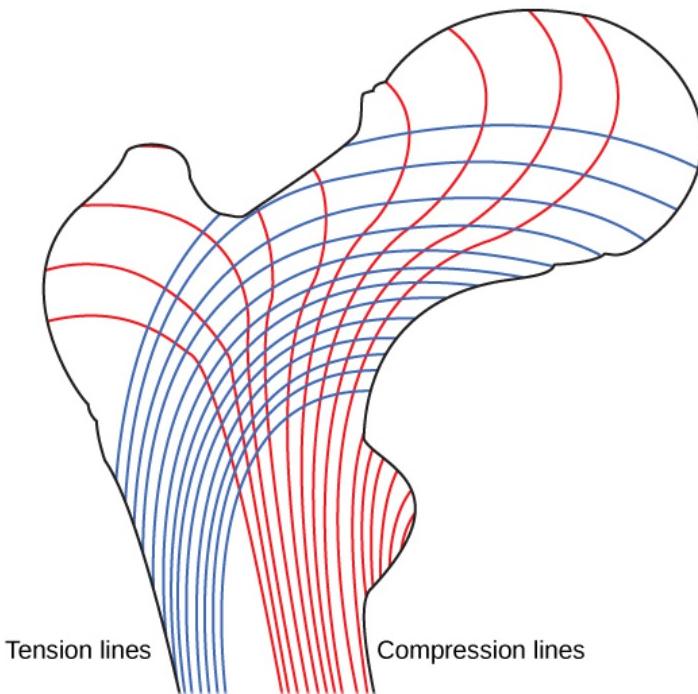
Spongy Bone Tissue

Whereas compact bone tissue forms the outer layer of all bones, **spongy bone** or cancellous bone forms the inner layer of all bones. Spongy bone tissue does not contain osteons that constitute compact bone tissue. Instead, it consists of **trabeculae**, which are lamellae that are arranged as rods or plates. Red bone marrow is found between the trabeculae. Blood vessels within this tissue deliver nutrients to osteocytes and remove waste. The red bone marrow of the femur and the interior of other large bones, such as the ileum, forms blood cells.

Spongy bone reduces the density of bone and allows the ends of long bones to compress as the result of stresses applied to the bone. Spongy bone is prominent in areas of bones that are not heavily stressed or where stresses arrive from many directions. The epiphyses of bones, such as the neck of the femur, are subject to stress from many directions. Imagine laying a heavy framed picture flat on the floor. You could hold up one side of the picture with a toothpick if the toothpick was perpendicular to the floor and the picture. Now drill a hole and stick the toothpick into the wall to hang up the picture. In this case, the function of the toothpick is to transmit the downward pressure of the picture to the wall. The force on the picture is straight down to the floor, but the force on the toothpick is both the picture wire pulling down and

the bottom of the hole in the wall pushing up. The toothpick will break off right at the wall.

The neck of the femur is horizontal like the toothpick in the wall. The weight of the body pushes it down near the joint, but the vertical diaphysis of the femur pushes it up at the other end. The neck of the femur must be strong enough to transfer the downward force of the body weight horizontally to the vertical shaft of the femur ([\[link\]](#)).



Link to Learning

View [micrographs](#) of musculoskeletal tissues as you review the anatomy.

Cell Types in Bones

Bone consists of four types of cells: osteoblasts, osteoclasts, osteocytes, and osteoprogenitor cells.

Osteoblasts are bone cells that are responsible for bone formation. Osteoblasts synthesize and secrete the organic part and inorganic part of the extracellular matrix of bone tissue, and collagen fibers. Osteoblasts become trapped in these secretions and differentiate into less active osteocytes. **Osteoclasts** are large bone cells with up to 50 nuclei. They remove bone structure by releasing lysosomal enzymes and acids that dissolve the bony matrix. These minerals, released from bones into the blood, help regulate calcium concentrations in body fluids. Bone may also be resorbed for remodeling, if the applied stresses have changed. **Osteocytes** are mature bone cells and are the main cells in bony connective tissue; these cells cannot divide. Osteocytes maintain normal bone structure by recycling the mineral salts in the bony matrix. **Osteoprogenitor cells** are squamous stem cells that divide to produce daughter cells that differentiate into osteoblasts. Osteoprogenitor cells are important in the repair of fractures.

Development of Bone

Ossification, or osteogenesis, is the process of bone formation by osteoblasts. Ossification is distinct from the process of calcification; whereas calcification takes place during the ossification of bones, it can also occur in other tissues. Ossification begins approximately six weeks after fertilization in an embryo. Before this time, the embryonic skeleton consists entirely of fibrous membranes and hyaline cartilage. The development of bone from fibrous membranes is called intramembranous ossification; development from hyaline cartilage is called endochondral ossification. Bone growth continues until approximately age 25. Bones can grow in thickness throughout life, but after age 25, ossification functions primarily in bone remodeling and repair.

Endochondral ossification is the process of bone development from hyaline cartilage. The periosteum is the connective tissue on the outside of bone that acts as the interface between bone, blood vessels, tendons, and ligaments.

Intramembranous Ossification

Intramembranous ossification is the process of bone development from fibrous membranes. It is involved in the formation of the flat bones of the skull, the mandible, and the clavicles. Ossification begins as mesenchymal cells form a template of the future bone. They then differentiate into osteoblasts at the ossification center. Osteoblasts secrete the

extracellular matrix and deposit calcium, which hardens the matrix. The non-mineralized portion of the bone or osteoid continues to form around blood vessels, forming spongy bone. Connective tissue in the matrix differentiates into red bone marrow in the fetus. The spongy bone is remodeled into a thin layer of compact bone on the surface of the spongy bone.

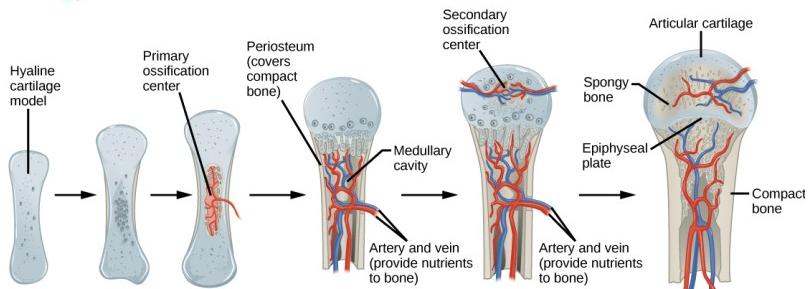
Endochondral Ossification

Endochondral ossification is the process of bone development from hyaline cartilage. All of the bones of the body, except for the flat bones of the skull, mandible, and clavicles, are formed through endochondral ossification.

In long bones, chondrocytes form a template of the hyaline cartilage diaphysis. Responding to complex developmental signals, the matrix begins to calcify. This calcification prevents diffusion of nutrients into the matrix, resulting in chondrocytes dying and the opening up of cavities in the diaphysis cartilage. Blood vessels invade the cavities, and osteoblasts and osteoclasts modify the calcified cartilage matrix into spongy bone. Osteoclasts then break down some of the spongy bone to create a marrow, or medullary, cavity in the center of the diaphysis. Dense, irregular connective tissue forms a sheath (periosteum) around the bones. The periosteum assists in attaching the bone to surrounding tissues,

tendons, and ligaments. The bone continues to grow and elongate as the cartilage cells at the epiphyses divide.

In the last stage of prenatal bone development, the centers of the epiphyses begin to calcify. Secondary ossification centers form in the epiphyses as blood vessels and osteoblasts enter these areas and convert hyaline cartilage into spongy bone. Until adolescence, hyaline cartilage persists at the **epiphyseal plate** (growth plate), which is the region between the diaphysis and epiphysis that is responsible for the lengthwise growth of long bones ([\[link\]](#)).



Growth of Bone

Long bones continue to lengthen, potentially until adolescence, through the addition of bone tissue at the epiphyseal plate. They also increase in width through appositional growth.

Lengthening of Long Bones

Chondrocytes on the epiphyseal side of the epiphyseal plate divide; one cell remains undifferentiated near the epiphysis, and one cell moves toward the diaphysis. The cells, which are pushed from the epiphysis, mature and are destroyed by calcification. This process replaces cartilage with bone on the diaphyseal side of the plate, resulting in a lengthening of the bone.

Long bones stop growing at around the age of 18 in females and the age of 21 in males in a process called epiphyseal plate closure. During this process, cartilage cells stop dividing and all of the cartilage is replaced by bone. The epiphyseal plate fades, leaving a structure called the epiphyseal line or epiphyseal remnant, and the epiphysis and diaphysis fuse.

Thickening of Long Bones

Appositional growth is the increase in the diameter of bones by the addition of bony tissue at the surface of bones. Osteoblasts at the bone surface secrete bone matrix, and osteoclasts on the inner surface break down bone. The osteoblasts differentiate into osteocytes. A balance between these two processes allows the bone to thicken without becoming too heavy.

After this bone is set, a callus will knit the two ends together. (credit: Bill Rhodes)

Bone Remodeling and Repair

Bone renewal continues after birth into adulthood. **Bone remodeling** is the replacement of old bone tissue by new bone tissue. It involves the processes of bone deposition by osteoblasts and bone resorption by osteoclasts. Normal bone growth requires vitamins D, C, and A, plus minerals such as calcium, phosphorous, and magnesium. Hormones such as parathyroid hormone, growth hormone, and calcitonin are also required for proper bone growth and maintenance.

Bone turnover rates are quite high, with five to seven percent of bone mass being recycled every week. Differences in turnover rate exist in different areas of the skeleton and in different areas of a bone. For example, the bone in the head of the femur may be fully replaced every six months, whereas the bone along the shaft is altered much more slowly.

Bone remodeling allows bones to adapt to stresses by becoming thicker and stronger when subjected to stress. Bones that are not subject to normal stress, for example when a limb is in a cast, will begin to lose mass. A fractured or broken bone undergoes repair through four stages:

1. Blood vessels in the broken bone tear and hemorrhage, resulting in the formation of

clotted blood, or a hematoma, at the site of the break. The severed blood vessels at the broken ends of the bone are sealed by the clotting process, and bone cells that are deprived of nutrients begin to die.

2. Within days of the fracture, capillaries grow into the hematoma, and phagocytic cells begin to clear away the dead cells. Though fragments of the blood clot may remain, fibroblasts and osteoblasts enter the area and begin to reform bone. Fibroblasts produce collagen fibers that connect the broken bone ends, and osteoblasts start to form spongy bone. The repair tissue between the broken bone ends is called the fibrocartilaginous callus, as it is composed of both hyaline and fibrocartilage ([\[link\]](#)). Some bone spicules may also appear at this point.
3. The fibrocartilaginous callus is converted into a bony callus of spongy bone. It takes about two months for the broken bone ends to be firmly joined together after the fracture. This is similar to the endochondral formation of bone, as cartilage becomes ossified; osteoblasts, osteoclasts, and bone matrix are present.
4. The bony callus is then remodelled by osteoclasts and osteoblasts, with excess material on the exterior of the bone and within the medullary cavity being removed. Compact bone is added to create bone tissue that is similar to the original, unbroken bone. This remodeling can take many months, and the

bone may remain uneven for years.



Scientific Method Connection

Decalcification of Bones

Question: What effect does the removal of calcium and collagen have on bone structure?

Background: Conduct a literature search on the role of calcium and collagen in maintaining bone structure. Conduct a literature search on diseases in which bone structure is compromised.

Hypothesis: Develop a hypothesis that states predictions of the flexibility, strength, and mass of bones that have had the calcium and collagen components removed. Develop a hypothesis

regarding the attempt to add calcium back to decalcified bones.

Test the hypothesis: Test the prediction by removing calcium from chicken bones by placing them in a jar of vinegar for seven days. Test the hypothesis regarding adding calcium back to decalcified bone by placing the decalcified chicken bones into a jar of water with calcium supplements added. Test the prediction by denaturing the collagen from the bones by baking them at 250°C for three hours.

Analyze the data: Create a table showing the changes in bone flexibility, strength, and mass in the three different environments.

Report the results: Under which conditions was the bone most flexible? Under which conditions was the bone the strongest?

Draw a conclusion: Did the results support or refute the hypothesis? How do the results observed in this experiment correspond to diseases that destroy bone tissue?

Section Summary

Bone, or osseous tissue, is connective tissue that includes specialized cells, mineral salts, and collagen fibers. The human skeleton can be divided

into long bones, short bones, flat bones, and irregular bones. Compact bone tissue is composed of osteons and forms the external layer of all bones. Spongy bone tissue is composed of trabeculae and forms the inner part of all bones. Four types of cells compose bony tissue: osteocytes, osteoclasts, osteoprogenitor cells, and osteoblasts. Ossification is the process of bone formation by osteoblasts. Intramembranous ossification is the process of bone development from fibrous membranes. Endochondral ossification is the process of bone development from hyaline cartilage. Long bones lengthen as chondrocytes divide and secrete hyaline cartilage. Osteoblasts replace cartilage with bone. Appositional growth is the increase in the diameter of bones by the addition of bone tissue at the surface of bones. Bone remodeling involves the processes of bone deposition by osteoblasts and bone resorption by osteoclasts. Bone repair occurs in four stages and can take several months.

Art Exercise

[\[link\]](#) Which of the following statements about bone tissue is false?

1. Compact bone tissue is made of cylindrical osteons that are aligned such that they

- travel the length of the bone.
2. Haversian canals contain blood vessels only.
 3. Haversian canals contain blood vessels and nerve fibers.
 4. Spongy tissue is found on the interior of the bone, and compact bone tissue is found on the exterior.
-

[\[link\]](#)B

Review Questions

The Haversian canal:

1. is arranged as rods or plates
 2. contains the bone's blood vessels and nerve fibers
 3. is responsible for the lengthwise growth of long bones
 4. synthesizes and secretes matrix
-

B

The epiphyseal plate:

-
1. is arranged as rods or plates
 2. contains the bone's blood vessels and nerve fibers
 3. is responsible for the lengthwise growth of long bones
 4. synthesizes and secretes bone matrix

C

The cells responsible for bone resorption are _____.

1. osteoclasts
 2. osteoblasts
 3. fibroblasts
 4. osteocytes
-

A

Compact bone is composed of _____.

1. trabeculae
 2. compacted collagen
 3. osteons
 4. calcium phosphate only
-

C

Osteoporosis is a condition where bones become weak and brittle. It is caused by an imbalance in the activity of which cells?

1. osteoclasts and osteoblasts
 2. osteoclasts and osteocytes
 3. osteoblasts and chondrocytes
 4. osteocytes and chondrocytes
-

A

While assembling a skeleton of a new species, a scientist points to one of the bones and observes that it looks like the most likely site of leg muscle attachment. What kind of bone did she indicate?

1. sesamoid bone
 2. long bone
 3. trabecular bone
 4. flat bone
-

D

Critical Thinking Questions

What are the major differences between spongy bone and compact bone?

Compact bone tissue forms the hard external layer of all bones and consists of osteons.

Compact bone tissue is prominent in areas of bone at which stresses are applied in only a few directions. Spongy bone tissue forms the inner layer of all bones and consists of trabeculae.

Spongy bone is prominent in areas of bones that are not heavily stressed or at which stresses arrive from many directions.

What are the roles of osteoblasts, osteocytes, and osteoclasts?

Osteocytes function in the exchange of nutrients and wastes with the blood. They also maintain normal bone structure by recycling the mineral salts in the bony matrix. Osteoclasts remove bone tissue by releasing lysosomal enzymes and acids that dissolve the bony matrix. Osteoblasts are bone cells that are responsible for bone formation.

Thalidomide was a morning sickness drug given to women that caused babies to be born without arm bones. If recent studies have

shown that thalidomide prevents the formation of new blood vessels, describe the type of bone development inhibited by the drug and what stage of ossification was affected.

Thalidomide effected the development of the long bones of the arms, disrupting endochondral ossification. The bones would have been able to develop into a template made of the calcified cartilage matrix, but new blood vessels could not be created. Since no vessels invade the template, the structure is not converted into trabecular bone.

Glossary

appositional growth

increase in the diameter of bones by the addition of bone tissue at the surface of bones

bone

(also, osseous tissue) connective tissue that constitutes the endoskeleton

bone remodeling

replacement of old bone tissue by new bone tissue

calcification

process of deposition of mineral salts in the

collagen fiber matrix that crystallizes and hardens the tissue

compact bone

forms the hard external layer of all bones

diaphysis

central shaft of bone, contains bone marrow in a marrow cavity

endochondral ossification

process of bone development from hyaline cartilage

epiphyseal plate

region between the diaphysis and epiphysis that is responsible for the lengthwise growth of long bones

epiphysis

rounded end of bone, covered with articular cartilage and filled with red bone marrow, which produces blood cells

flat bone

thin and relatively broad bone found where extensive protection of organs is required or where broad surfaces of muscle attachment are required

Haversian canal

contains the bone's blood vessels and nerve

fibers

intramembranous ossification

process of bone development from fibrous membranes

irregular bone

bone with complex shapes; examples include vertebrae and hip bones

lamella

layer of compact tissue that surrounds a central canal called the Haversian canal

long bone

bone that is longer than wide, and has a shaft and two ends

osteoblast

bone cell responsible for bone formation

osteoclast

large bone cells with up to 50 nuclei, responsible for bone remodeling

osteocyte

mature bone cells and the main cell in bone tissue

osseous tissue

connective tissue that constitutes the endoskeleton

ossification

(also, osteogenesis) process of bone formation by osteoblasts

osteon

cylindrical structure aligned parallel to the long axis of the bone

resorption

process by which osteoclasts release minerals stored in bones

sesamoid bone

small, flat bone shaped like a sesame seed; develops inside tendons

short bone

bone that has the same width and length, giving it a cube-like shape

spongy bone tissue

forms the inner layer of all bones

sutural bone

small, flat, irregularly shaped bone that forms between the flat bones of the cranium

trabeculae

lamellae that are arranged as rods or plates

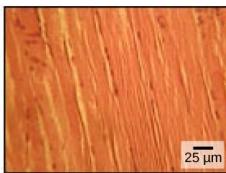
Muscle Contraction and Locomotion

By the end of this section, you will be able to do the following:

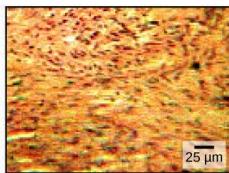
- Classify the different types of muscle tissue
- Explain the role of muscles in locomotion

Muscle cells are specialized for contraction. Muscles allow for motions such as walking, and they also facilitate bodily processes such as respiration and digestion. The body contains three types of muscle tissue: skeletal muscle, cardiac muscle, and smooth muscle ([\[link\]](#)).

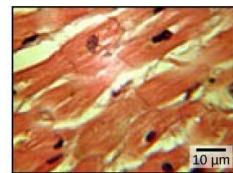
The body contains three types of muscle tissue: skeletal muscle, smooth muscle, and cardiac muscle, visualized here using light microscopy. Smooth muscle cells are short, tapered at each end, and have only one plump nucleus in each. Cardiac muscle cells are branched and striated, but short. The cytoplasm may branch, and they have one nucleus in the center of the cell. (credit: modification of work by NCI, NIH; scale-bar data from Matt Russell)



Skeletal muscle



Smooth muscle



Cardiac muscle

Skeletal muscle tissue forms skeletal muscles, which attach to bones or skin and control

locomotion and any movement that can be consciously controlled. Because it can be controlled by thought, skeletal muscle is also called voluntary muscle. Skeletal muscles are long and cylindrical in appearance; when viewed under a microscope, skeletal muscle tissue has a striped or striated appearance. The striations are caused by the regular arrangement of contractile proteins (actin and myosin). **Actin** is a globular contractile protein that interacts with **myosin** for muscle contraction. Skeletal muscle also has multiple nuclei present in a single cell.

Smooth muscle tissue occurs in the walls of hollow organs such as the intestines, stomach, and urinary bladder, and around passages such as the respiratory tract and blood vessels. Smooth muscle has no striations, is not under voluntary control, has only one nucleus per cell, is tapered at both ends, and is called involuntary muscle.

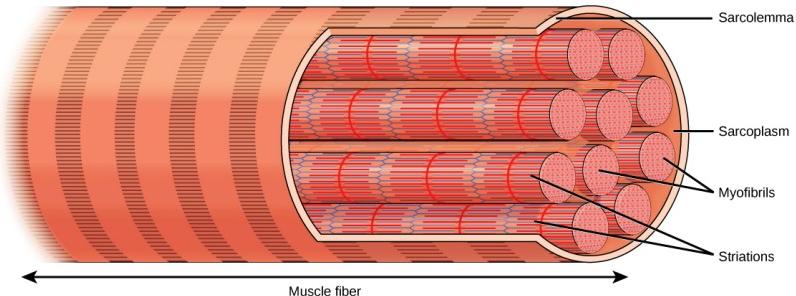
Cardiac muscle tissue is only found in the heart, and cardiac contractions pump blood throughout the body and maintain blood pressure. Like skeletal muscle, cardiac muscle is striated, but unlike skeletal muscle, cardiac muscle cannot be consciously controlled and is called involuntary muscle. It has one nucleus per cell, is branched, and is distinguished by the presence of intercalated disks.

A skeletal muscle cell is surrounded by a plasma

membrane called the sarcolemma with a cytoplasm called the sarcoplasm. A muscle fiber is composed of many fibrils, packaged into orderly units. A sarcomere is the region from one Z line to the next Z line. Many sarcomeres are present in a myofibril, resulting in the striation pattern characteristic of skeletal muscle.

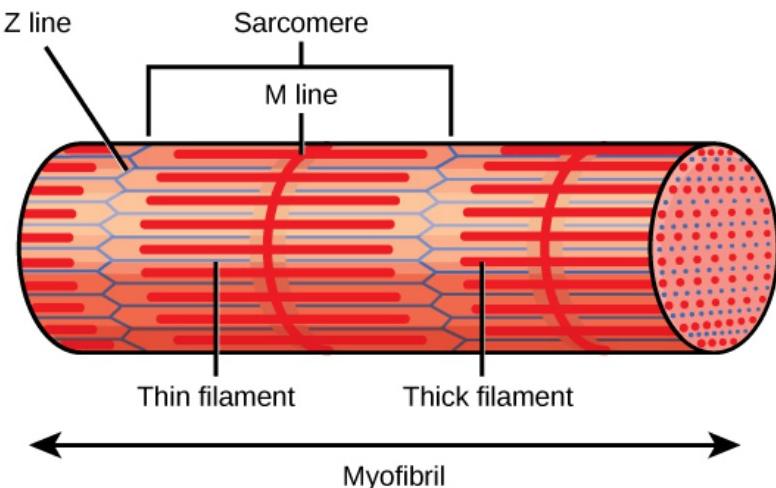
Skeletal Muscle Fiber Structure

Each skeletal muscle fiber is a skeletal muscle cell. These cells are incredibly large, with diameters of up to 100 μm and lengths of up to 30 cm. The plasma membrane of a skeletal muscle fiber is called the **sarcolemma**. The sarcolemma is the site of action potential conduction, which triggers muscle contraction. Within each muscle fiber are **myofibrils**—long cylindrical structures that lie parallel to the muscle fiber. Myofibrils run the entire length of the muscle fiber, and because they are only approximately 1.2 μm in diameter, hundreds to thousands can be found inside one muscle fiber. They attach to the sarcolemma at their ends, so that as myofibrils shorten, the entire muscle cell contracts ([\[link\]](#)).



The striated appearance of skeletal muscle tissue is a result of repeating bands of the proteins actin and myosin that are present along the length of myofibrils. Dark A bands and light I bands repeat along myofibrils, and the alignment of myofibrils in the cell causes the entire cell to appear striated or banded.

Each I band has a dense line running vertically through the middle called a Z disc or Z line. The Z discs mark the border of units called **sarcomeres**, which are the functional units of skeletal muscle. One sarcomere is the space between two consecutive Z discs and contains one entire A band and two halves of an I band, one on either side of the A band. A myofibril is composed of many sarcomeres running along its length, and as the sarcomeres individually contract, the myofibrils and muscle cells shorten ([\[link\]](#)).



Myofibrils are composed of smaller structures called **myofilaments**. There are two main types of filaments: thick filaments and thin filaments; each has different compositions and locations. **Thick filaments** occur only in the A band of a myofibril. **Thin filaments** attach to a protein in the Z disc called alpha-actinin and occur across the entire length of the I band and partway into the A band. The region at which thick and thin filaments overlap has a dense appearance, as there is little space between the filaments. Thin filaments do not extend all the way into the A bands, leaving a central region of the A band that only contains thick filaments. This central region of the A band looks slightly lighter than the rest of the A band and is called the H zone. The middle of the H zone has a vertical line called the M line, at which accessory proteins hold together thick filaments. Both the Z disc and the M line hold myofilaments in place to

maintain the structural arrangement and layering of the myofibril. Myofibrils are connected to each other by intermediate, or desmin, filaments that attach to the Z disc.

Thick and thin filaments are themselves composed of proteins. Thick filaments are composed of the protein myosin. The tail of a myosin molecule connects with other myosin molecules to form the central region of a thick filament near the M line, whereas the heads align on either side of the thick filament where the thin filaments overlap. The primary component of thin filaments is the actin protein. Two other components of the thin filament are tropomyosin and troponin. Actin has binding sites for myosin attachment. Strands of tropomyosin block the binding sites and prevent actin–myosin interactions when the muscles are at rest. Troponin consists of three globular subunits. One subunit binds to tropomyosin, one subunit binds to actin, and one subunit binds Ca^{2+} ions.

Link to Learning

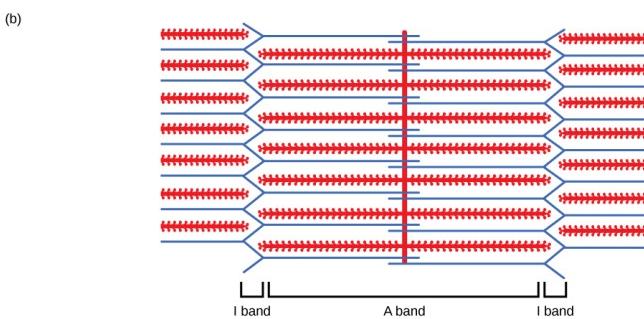
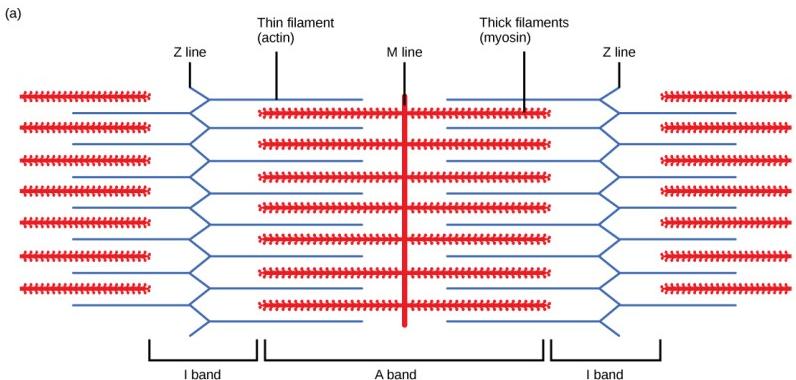
View this animation showing the organization of muscle fibers.

https://www.openstax.org/l/skeletal_muscle

When (a) a sarcomere (b) contracts, the Z lines move closer together and the I band gets smaller. The A band stays the same width and, at full contraction, the thin filaments overlap.

Sliding Filament Model of Contraction

For a muscle cell to contract, the sarcomere must shorten. However, thick and thin filaments—the components of sarcomeres—do not shorten. Instead, they slide by one another, causing the sarcomere to shorten while the filaments remain the same length. The sliding filament theory of muscle contraction was developed to fit the differences observed in the named bands on the sarcomere at different degrees of muscle contraction and relaxation. The mechanism of contraction is the binding of myosin to actin, forming cross-bridges that generate filament movement ([\[link\]](#)).



When a sarcomere shortens, some regions shorten whereas others stay the same length. A sarcomere is defined as the distance between two consecutive Z discs or Z lines; when a muscle contracts, the distance between the Z discs is reduced. The H zone—the central region of the A zone—contains only thick filaments and is shortened during contraction. The I band contains only thin filaments and also shortens. The A band does not shorten—it remains the same length—but A bands of different sarcomeres move closer together during contraction, eventually disappearing. Thin filaments are pulled by the thick filaments toward the center of the sarcomere until the Z discs approach the thick

filaments. The zone of overlap, in which thin filaments and thick filaments occupy the same area, increases as the thin filaments move inward.

ATP and Muscle Contraction

The motion of muscle shortening occurs as myosin heads bind to actin and pull the actin inwards. This action requires energy, which is provided by ATP. Myosin binds to actin at a binding site on the globular actin protein. Myosin has another binding site for ATP at which enzymatic activity hydrolyzes ATP to ADP, releasing an inorganic phosphate molecule and energy.

ATP binding causes myosin to release actin, allowing actin and myosin to detach from each other. After this happens, the newly bound ATP is converted to ADP and inorganic phosphate, Pi. The enzyme at the binding site on myosin is called ATPase. The energy released during ATP hydrolysis changes the angle of the myosin head into a “cocked” position. The myosin head is then in a position for further movement, possessing potential energy, but ADP and Pi are still attached. If actin binding sites are covered and unavailable, the myosin will remain in the high energy configuration with ATP hydrolyzed, but still attached.

If the actin binding sites are uncovered, a cross-

bridge will form; that is, the myosin head spans the distance between the actin and myosin molecules. Pi is then released, allowing myosin to expend the stored energy as a conformational change. The myosin head moves toward the M line, pulling the actin along with it. As the actin is pulled, the filaments move approximately 10 nm toward the M line. This movement is called the power stroke, as it is the step at which force is produced. As the actin is pulled toward the M line, the sarcomere shortens and the muscle contracts.

When the myosin head is “cocked,” it contains energy and is in a high-energy configuration. This energy is expended as the myosin head moves through the power stroke; at the end of the power stroke, the myosin head is in a low-energy position. After the power stroke, ADP is released; however, the cross-bridge formed is still in place, and actin and myosin are bound together. ATP can then attach to myosin, which allows the cross-bridge cycle to start again and further muscle contraction can occur ([\[link\]](#)).

Link to Learning

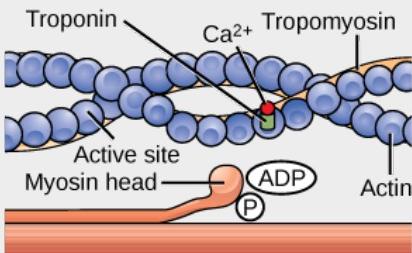
Watch this video explaining how a muscle contraction is signaled.

https://www.openstax.org/l/contract_muscle

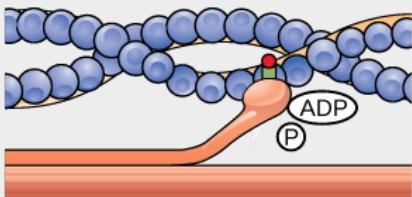
Visual Connection

The cross-bridge muscle contraction cycle, which is triggered by Ca^{2+} binding to the actin active site, is shown. With each contraction cycle, actin moves relative to myosin.

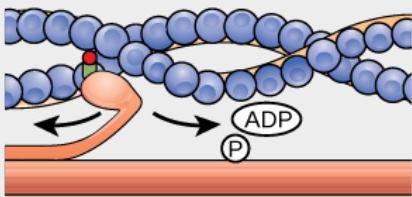
- ① The active site on actin is exposed as Ca^{2+} binds troponin.



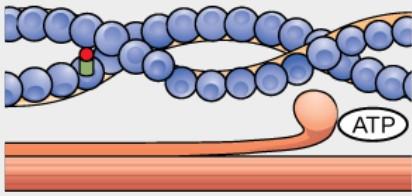
- ② The myosin head forms a cross-bridge with actin.



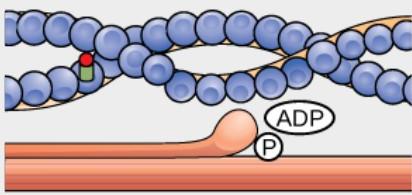
- ③ During the power stroke, the myosin head bends, and ADP and phosphate are released.



- ④ A new molecule of ATP attaches to the myosin head, causing the cross-bridge to detach.



- ⑤ ATP hydrolyzes to ADP and phosphate, which returns the myosin to the "cocked" position.



Which of the following statements about muscle

contraction is true?

1. The power stroke occurs when ATP is hydrolyzed to ADP and phosphate.
2. The power stroke occurs when ADP and phosphate dissociate from the myosin head.
3. The power stroke occurs when ADP and phosphate dissociate from the actin active site.
4. The power stroke occurs when Ca^{2+} binds the calcium head.

Link to Learning

View this [animation](#) of the cross-bridge muscle contraction.

Regulatory Proteins

When a muscle is in a resting state, actin and myosin are separated. To keep actin from binding to the active site on myosin, regulatory proteins block the molecular binding sites. **Tropomyosin** blocks myosin binding sites on actin molecules, preventing cross-bridge formation and preventing contraction in a muscle without nervous input. **Troponin** binds

to tropomyosin and helps to position it on the actin molecule; it also binds calcium ions.

To enable a muscle contraction, tropomyosin must change conformation, uncovering the myosin-binding site on an actin molecule and allowing cross-bridge formation. This can only happen in the presence of calcium, which is kept at extremely low concentrations in the sarcoplasm. If present, calcium ions bind to troponin, causing conformational changes in troponin that allow tropomyosin to move away from the myosin binding sites on actin. Once the tropomyosin is removed, a cross-bridge can form between actin and myosin, triggering contraction. Cross-bridge cycling continues until Ca^{2+} ions and ATP are no longer available and tropomyosin again covers the binding sites on actin.

Excitation–Contraction Coupling

Excitation–contraction coupling is the link (transduction) between the action potential generated in the sarcolemma and the start of a muscle contraction. The trigger for calcium release from the sarcoplasmic reticulum into the sarcoplasm is a neural signal. Each skeletal muscle fiber is controlled by a motor neuron, which conducts signals from the brain or spinal cord to the muscle. The area of the sarcolemma on the muscle fiber that interacts with the neuron is called the **motor end**.

plate. The end of the neuron's axon is called the synaptic terminal, and it does not actually contact the motor end plate. A small space called the synaptic cleft separates the synaptic terminal from the motor end plate. Electrical signals travel along the neuron's axon, which branches through the muscle and connects to individual muscle fibers at a neuromuscular junction.

The ability of cells to communicate electrically requires that the cells expend energy to create an electrical gradient across their cell membranes. This charge gradient is carried by ions, which are differentially distributed across the membrane. Each ion exerts an electrical influence and a concentration influence. Just as milk will eventually mix with coffee without the need to stir, ions also distribute themselves evenly, if they are permitted to do so. In this case, they are not permitted to return to an evenly mixed state.

The sodium–potassium ATPase uses cellular energy to move K^+ ions inside the cell and Na^+ ions outside. This alone accumulates a small electrical charge, but a big concentration gradient. There is lots of K^+ in the cell and lots of Na^+ outside the cell. Potassium is able to leave the cell through K^+ channels that are open 90% of the time, and it does. However, Na^+ channels are rarely open, so Na^+ remains outside the cell. When K^+ leaves the cell, obeying its concentration gradient, that effectively

leaves a negative charge behind. So at rest, there is a large concentration gradient for Na^+ to enter the cell, and there is an accumulation of negative charges left behind in the cell. This is the resting membrane potential. Potential in this context means a separation of electrical charge that is capable of doing work. It is measured in volts, just like a battery. However, the transmembrane potential is considerably smaller (0.07 V); therefore, the small value is expressed as millivolts (mV) or 70 mV. Because the inside of a cell is negative compared with the outside, a minus sign signifies the excess of negative charges inside the cell, -70 mV.

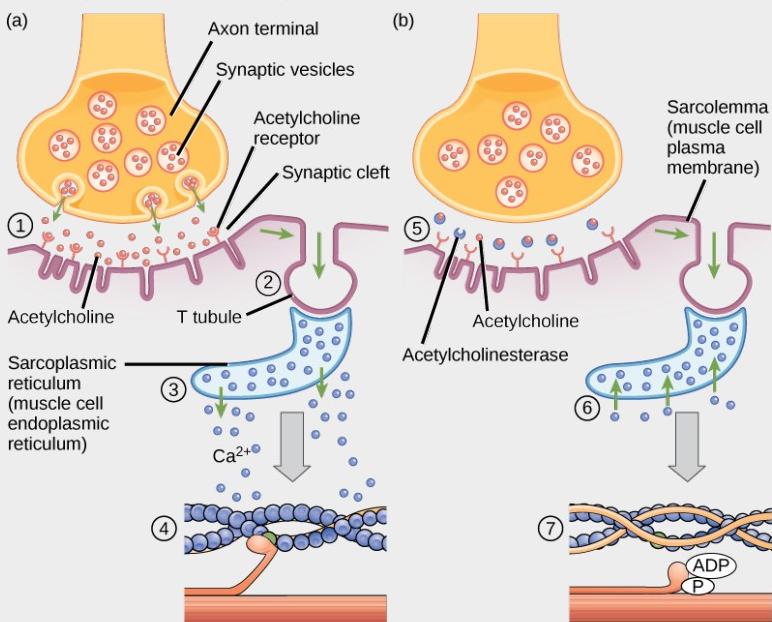
If an event changes the permeability of the membrane to Na^+ ions, they will enter the cell. That will change the voltage. This is an electrical event, called an action potential, that can be used as a cellular signal. Communication occurs between nerves and muscles through neurotransmitters. Neuron action potentials cause the release of neurotransmitters from the synaptic terminal into the synaptic cleft, where they can then diffuse across the synaptic cleft and bind to a receptor molecule on the motor end plate. The motor end plate possesses junctional folds—folds in the sarcolemma that create a large surface area for the neurotransmitter to bind to receptors. The receptors are actually sodium channels that open to allow the passage of Na^+ into the cell when they receive a neurotransmitter signal.

Acetylcholine (ACh) is a neurotransmitter released by motor neurons that binds to receptors in the motor end plate. Neurotransmitter release occurs when an action potential travels down the motor neuron's axon, resulting in altered permeability of the synaptic terminal membrane and an influx of calcium. The Ca^{2+} ions allow synaptic vesicles to move to and bind with the presynaptic membrane (on the neuron), and release neurotransmitter from the vesicles into the synaptic cleft. Once released by the synaptic terminal, ACh diffuses across the synaptic cleft to the motor end plate, where it binds with ACh receptors. As a neurotransmitter binds, these ion channels open, and Na^+ ions cross the membrane into the muscle cell. This reduces the voltage difference between the inside and outside of the cell, which is called depolarization. As ACh binds at the motor end plate, this depolarization is called an end-plate potential. The depolarization then spreads along the sarcolemma, creating an action potential as sodium channels adjacent to the initial depolarization site sense the change in voltage and open. The action potential moves across the entire cell, creating a wave of depolarization.

ACh is broken down by the enzyme **acetylcholinesterase** (AChE) into acetyl and choline. AChE resides in the synaptic cleft, breaking down ACh so that it does not remain bound to ACh receptors, which would cause unwanted extended muscle contraction ([\[link\]](#)).

Visual Connection

This diagram shows excitation-contraction coupling in a skeletal muscle contraction. The sarcoplasmic reticulum is a specialized endoplasmic reticulum found in muscle cells.



1. Acetylcholine released from the axon terminal binds to receptors on the sarcolemma.
2. An action potential is generated and travels down the T tubule.
3. Ca^{2+} is released from the sarcoplasmic reticulum in response to the change in voltage.
4. Ca^{2+} binds troponin; Cross-bridges form between actin and myosin.
5. Acetylcholinesterase removes acetylcholine from the synaptic cleft.
6. Ca^{2+} is transported back into the sarcoplasmic reticulum.
7. Tropomyosin binds active sites on actin causing the cross-bridge to detach.

The deadly nerve gas Sarin irreversibly inhibits Acetylcholinesterase. What effect would Sarin have on muscle contraction?

After depolarization, the membrane returns to its

resting state. This is called repolarization, during which voltage-gated sodium channels close. Potassium channels continue at 90% conductance. Because the plasma membrane sodium–potassium ATPase always transports ions, the resting state (negatively charged inside relative to the outside) is restored. The period immediately following the transmission of an impulse in a nerve or muscle, in which a neuron or muscle cell regains its ability to transmit another impulse, is called the refractory period. During the refractory period, the membrane cannot generate another action potential. The refractory period allows the voltage-sensitive ion channels to return to their resting configurations. The sodium potassium ATPase continually moves Na^+ back out of the cell and K^+ back into the cell, and the K^+ leaks out leaving negative charge behind. Very quickly, the membrane repolarizes, so that it can again be depolarized.

Control of Muscle Tension

Neural control initiates the formation of actin–myosin cross-bridges, leading to the sarcomere shortening involved in muscle contraction. These contractions extend from the muscle fiber through connective tissue to pull on bones, causing skeletal movement. The pull exerted by a muscle is called tension, and the amount of force created by this tension can vary. This enables the same muscles to

move very light objects and very heavy objects. In individual muscle fibers, the amount of tension produced depends on the cross-sectional area of the muscle fiber and the frequency of neural stimulation.

The number of cross-bridges formed between actin and myosin determine the amount of tension that a muscle fiber can produce. Cross-bridges can only form where thick and thin filaments overlap, allowing myosin to bind to actin. If more cross-bridges are formed, more myosin will pull on actin, and more tension will be produced.

The ideal length of a sarcomere during production of maximal tension occurs when thick and thin filaments overlap to the greatest degree. If a sarcomere at rest is stretched past an ideal resting length, thick and thin filaments do not overlap to the greatest degree, and fewer cross-bridges can form. This results in fewer myosin heads pulling on actin, and less tension is produced. As a sarcomere is shortened, the zone of overlap is reduced as the thin filaments reach the H zone, which is composed of myosin tails. Because it is myosin heads that form cross-bridges, actin will not bind to myosin in this zone, reducing the tension produced by this myofiber. If the sarcomere is shortened even more, thin filaments begin to overlap with each other—reducing cross-bridge formation even further, and producing even less tension. Conversely, if the

sarcomere is stretched to the point at which thick and thin filaments do not overlap at all, no cross-bridges are formed and no tension is produced. This amount of stretching does not usually occur because accessory proteins, internal sensory nerves, and connective tissue oppose extreme stretching.

The primary variable determining force production is the number of myofibers within the muscle that receive an action potential from the neuron that controls that fiber. When using the biceps to pick up a pencil, the motor cortex of the brain only signals a few neurons of the biceps, and only a few myofibers respond. In vertebrates, each myofiber responds fully if stimulated. When picking up a piano, the motor cortex signals all of the neurons in the biceps and every myofiber participates. This is close to the maximum force the muscle can produce. As mentioned above, increasing the frequency of action potentials (the number of signals per second) can increase the force a bit more, because the tropomyosin is flooded with calcium.

Section Summary

The body contains three types of muscle tissue: skeletal muscle, cardiac muscle, and smooth muscle. Skeleton muscle tissue is composed of sarcomeres, the functional units of muscle tissue. Muscle contraction occurs when sarcomeres shorten, as

thick and thin filaments slide past each other, which is called the sliding filament model of muscle contraction. ATP provides the energy for cross-bridge formation and filament sliding. Regulatory proteins, such as troponin and tropomyosin, control cross-bridge formation. Excitation–contraction coupling transduces the electrical signal of the neuron, via acetylcholine, to an electrical signal on the muscle membrane, which initiates force production. The number of muscle fibers contracting determines how much force the whole muscle produces.

Visual Connection Questions

[\[link\]](#) Which of the following statements about muscle contraction is true?

1. The power stroke occurs when ATP is hydrolyzed to ADP and phosphate.
2. The power stroke occurs when ADP and phosphate dissociate from the myosin head.
3. The power stroke occurs when ADP and phosphate dissociate from the actin active site.
4. The power stroke occurs when Ca^{2+} binds the calcium head.

[\[link\]](#) B

[\[link\]](#) The deadly nerve gas Sarin irreversibly inhibits Acetylcholinesterase. What effect would Sarin have on muscle contraction?

[\[link\]](#) In the presence of Sarin, acetylcholine is not removed from the synapse, resulting in continuous stimulation of the muscle plasma membrane. At first, muscle activity is intense and uncontrolled, but the ion gradients dissipate, so electrical signals in the T-tubules are no longer possible. The result is paralysis, leading to death by asphyxiation.

Review Questions

In relaxed muscle, the myosin-binding site on actin is blocked by _____.

1. titin
 2. troponin
 3. myoglobin
 4. tropomyosin
-

D

The cell membrane of a muscle fiber is called a _____.

1. myofibril
 2. sarcolemma
 3. sarcoplasm
 4. myofilament
-

B

The muscle relaxes if no new nerve signal arrives. However the neurotransmitter from the previous stimulation is still present in the synapse. The activity of _____ helps to remove this neurotransmitter.

1. myosin
 2. action potential
 3. tropomyosin
 4. acetylcholinesterase
-

D

The ability of a muscle to generate tension immediately after stimulation is dependent on:

-
1. myosin interaction with the M line
 2. overlap of myosin and actin
 3. actin attachments to the Z line
 4. none of the above

D

Botulinum toxin causes flaccid paralysis of the muscles, and is used for cosmetic purposes under the name Botox. Which of the following is the most likely mechanism of action of Botox?

1. Botox decreases the production of acetylcholinesterase.
2. Botox increases calcium release from the sarcoplasmic reticulum.
3. Botox blocks the ATP binding site in actin.
4. Botox decreases the release of acetylcholine from motor neurons.

D

Critical Thinking Questions

How would muscle contractions be affected if ATP was completely depleted in a muscle fiber?

Because ATP is required for myosin to release from actin, muscles would remain rigidly contracted until more ATP was available for the myosin cross-bridge release. This is why dead vertebrates undergo rigor mortis.

What factors contribute to the amount of tension produced in an individual muscle fiber?

The cross-sectional area, the length of the muscle fiber at rest, and the frequency of neural stimulation.

What effect will low blood calcium have on neurons? What effect will low blood calcium have on skeletal muscles?

Neurons will not be able to release neurotransmitter without calcium. Skeletal muscles have calcium stored and don't need any from the outside.

Skeletal muscles can only produce a mechanical

force as they are contracted, but a leg flexes and extends while walking. How can muscles perform this task?

Muscles are able to drive locomotion (and other tasks involving opposing motions) because they are paired. When walking, the hamstring muscle contracts first, causing the leg to flex around the knee joint. The quadriceps muscle then contracts (while the hamstring relaxes and extends) to straighten the leg as the foot returns to the ground.

Glossary

actin

globular contractile protein that interacts with myosin for muscle contraction

acetylcholinesterase

(AChE) enzyme that breaks down ACh into acetyl and choline

cardiac muscle tissue

muscle tissue found only in the heart; cardiac contractions pump blood throughout the body and maintain blood pressure

motor end plate

sarcolemma of the muscle fiber that interacts

with the neuron

myofibril

long cylindrical structures that lie parallel to the muscle fiber

myofilament

small structures that make up myofibrils

myosin

contractile protein that interacts with actin for muscle contraction

sarcolemma

plasma membrane of a skeletal muscle fiber

sarcomere

functional unit of skeletal muscle

skeletal muscle tissue

forms skeletal muscles, which attach to bones and control locomotion and any movement that can be consciously controlled

smooth muscle tissue

occurs in the walls of hollow organs such as the intestines, stomach, and urinary bladder, and around passages such as the respiratory tract and blood vessels

thick filament

a group of myosin molecules

thin filament

two polymers of actin wound together along with tropomyosin and troponin

tropomyosin

acts to block myosin binding sites on actin molecules, preventing cross-bridge formation and preventing contraction until a muscle receives a neuron signal

troponin

binds to tropomyosin and helps to position it on the actin molecule, and also binds calcium ions

Digestive Systems

By the end of this section, you will be able to do the following:

- Explain the processes of digestion and absorption
- Compare and contrast different types of digestive systems
- Explain the specialized functions of the organs involved in processing food in the body
- Describe the ways in which organs work together to digest food and absorb nutrients

Animals obtain their nutrition from the consumption of other organisms. Depending on their diet, animals can be classified into the following categories: plant eaters (herbivores), meat eaters (carnivores), and those that eat both plants and animals (omnivores). The nutrients and macromolecules present in food are not immediately accessible to the cells. There are a number of processes that modify food within the animal body in order to make the nutrients and organic molecules accessible for cellular function. As animals evolved in complexity of form and function, their digestive systems have also evolved to accommodate their various dietary needs.

Herbivores, like this (a) mule deer and (b) monarch caterpillar, eat primarily plant material. (credit a: modification of work by Bill Ebbesen; credit b: modification of work by Doug Bowman) Carnivores like the (a) lion eat primarily meat. The (b) ladybug

is also a carnivore that consumes small insects called aphids. (credit a: modification of work by Kevin Pluck; credit b: modification of work by Jon Sullivan) Omnivores like the (a) bear and (b) crayfish eat both plant and animal based food. (credit a: modification of work by Dave Menke; credit b: modification of work by Jon Sullivan)

Herbivores, Omnivores, and Carnivores

Herbivores are animals whose primary food source is plant-based. Examples of herbivores, as shown in [\[link\]](#) include vertebrates like deer, koalas, and some bird species, as well as invertebrates such as crickets and caterpillars. These animals have evolved digestive systems capable of handling large amounts of plant material. Herbivores can be further classified into frugivores (fruit-eaters), granivores (seed eaters), nectivores (nectar feeders), and folivores (leaf eaters).



(a)



(b)

Carnivores are animals that eat other animals. The word carnivore is derived from Latin and literally means “meat eater.” Wild cats such as lions, shown in [link]a and tigers are examples of vertebrate carnivores, as are snakes and sharks, while invertebrate carnivores include sea stars, spiders, and ladybugs, shown in [link]b. Obligate carnivores are those that rely entirely on animal flesh to obtain their nutrients; examples of obligate carnivores are members of the cat family, such as lions and cheetahs. Facultative carnivores are those that also eat non-animal food in addition to animal food. Note that there is no clear line that differentiates facultative carnivores from omnivores; dogs would be considered facultative carnivores.



(a)



(b)

Omnivores are animals that eat both plant- and animal-derived food. In Latin, omnivore means to eat everything. Humans, bears (shown in [\[link\]a](#)), and chickens are example of vertebrate omnivores; invertebrate omnivores include cockroaches and crayfish (shown in [\[link\]b](#)).



(a)



(b)

(a) A gastrovascular cavity has a single opening through which food is ingested and waste is excreted, as shown in this hydra and in this jellyfish medusa. (b) An alimentary canal has two openings: a mouth for ingesting food, and an anus for eliminating waste, as shown in this nematode.

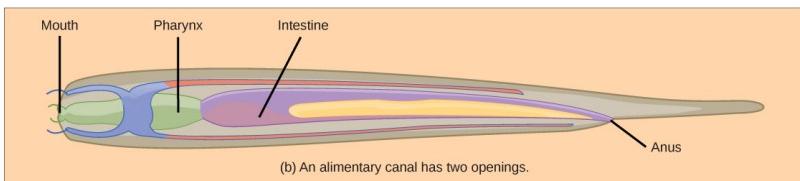
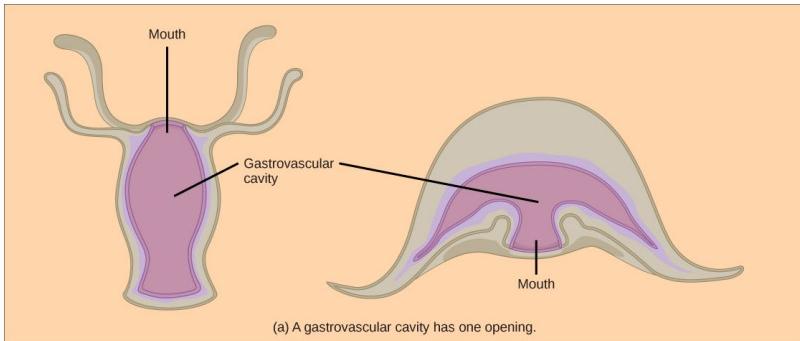
Invertebrate Digestive Systems

Animals have evolved different types of digestive systems to aid in the digestion of the different foods they consume. The simplest example is that of a **gastrovascular cavity** and is found in organisms with only one opening for digestion.

Platyhelminthes (flatworms), Ctenophora (comb jellies), and Cnidaria (coral, jelly fish, and sea anemones) use this type of digestion. Gastrovascular cavities, as shown in [\[link\]a](#), are typically a blind tube or cavity with only one opening, the “mouth”, which also serves as an “anus”. Ingested material enters the mouth and passes through a hollow, tubular cavity. Cells within the cavity secrete digestive enzymes that breakdown the food. The food particles are engulfed by the cells lining the gastrovascular cavity.

The **alimentary canal**, shown in [\[link\]b](#), is a more advanced system: it consists of one tube with a mouth at one end and an anus at the other.

Earthworms are an example of an animal with an alimentary canal. Once the food is ingested through the mouth, it passes through the esophagus and is stored in an organ called the crop; then it passes into the gizzard where it is churned and digested. From the gizzard, the food passes through the intestine, the nutrients are absorbed, and the waste is eliminated as feces, called castings, through the anus.



(a) Humans and herbivores, such as the (b) rabbit, have a monogastric digestive system. However, in the rabbit the small intestine and cecum are enlarged to allow more time to digest plant material. The enlarged organ provides more surface area for absorption of nutrients. Rabbits digest their food twice: the first time food passes through the digestive system, it collects in the cecum, and then it passes as soft feces called cecotrophes. The rabbit re-ingests these cecotrophes to further digest them. The avian esophagus has a pouch, called a crop, which stores food. Food passes from the crop to the first of two stomachs, called the proventriculus, which contains digestive juices that breakdown food. From the proventriculus, the food enters the second stomach, called the gizzard, which grinds food. Some birds swallow stones or grit, which are stored in the gizzard, to aid the grinding process. Birds do not have separate openings to excrete urine

and feces. Instead, uric acid from the kidneys is secreted into the large intestine and combined with waste from the digestive process. This waste is excreted through an opening called the cloaca. Ruminant animals, such as goats and cows, have four stomachs. The first two stomachs, the rumen and the reticulum, contain prokaryotes and protists that are able to digest cellulose fiber. The ruminant regurgitates cud from the reticulum, chews it, and swallows it into a third stomach, the omasum, which removes water. The cud then passes onto the fourth stomach, the abomasum, where it is digested by enzymes produced by the ruminant.

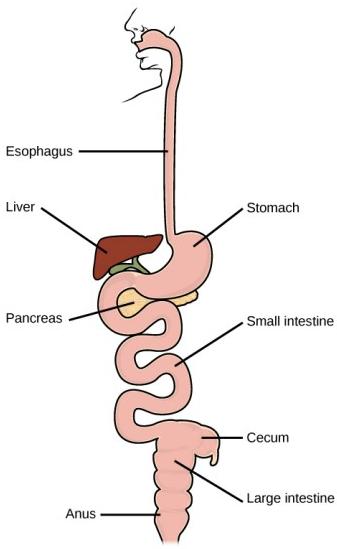
Vertebrate Digestive Systems

Vertebrates have evolved more complex digestive systems to adapt to their dietary needs. Some animals have a single stomach, while others have multi-chambered stomachs. Birds have developed a digestive system adapted to eating unmasticated food.

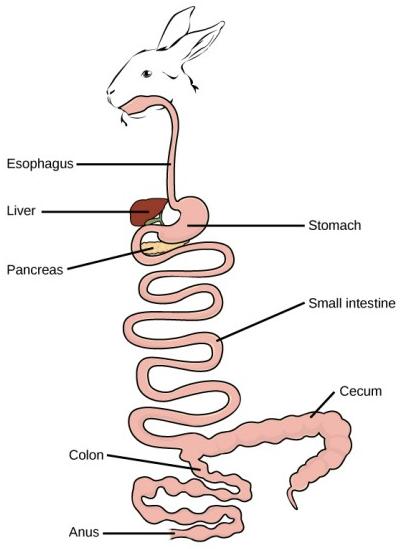
Monogastric: Single-chambered Stomach

As the word **monogastric** suggests, this type of digestive system consists of one (“mono”) stomach chamber (“gastric”). Humans and many animals have a monogastric digestive system as illustrated in [\[link\]ab](#). The process of digestion begins with the

mouth and the intake of food. The teeth play an important role in masticating (chewing) or physically breaking down food into smaller particles. The enzymes present in saliva also begin to chemically breakdown food. The esophagus is a long tube that connects the mouth to the stomach. Using peristalsis, or wave-like smooth muscle contractions, the muscles of the esophagus push the food towards the stomach. In order to speed up the actions of enzymes in the stomach, the stomach is an extremely acidic environment, with a pH between 1.5 and 2.5. The gastric juices, which include enzymes in the stomach, act on the food particles and continue the process of digestion. Further breakdown of food takes place in the small intestine where enzymes produced by the liver, the small intestine, and the pancreas continue the process of digestion. The nutrients are absorbed into the bloodstream across the epithelial cells lining the walls of the small intestines. The waste material travels on to the large intestine where water is absorbed and the drier waste material is compacted into feces; it is stored until it is excreted through the rectum.



(a) Human digestive system

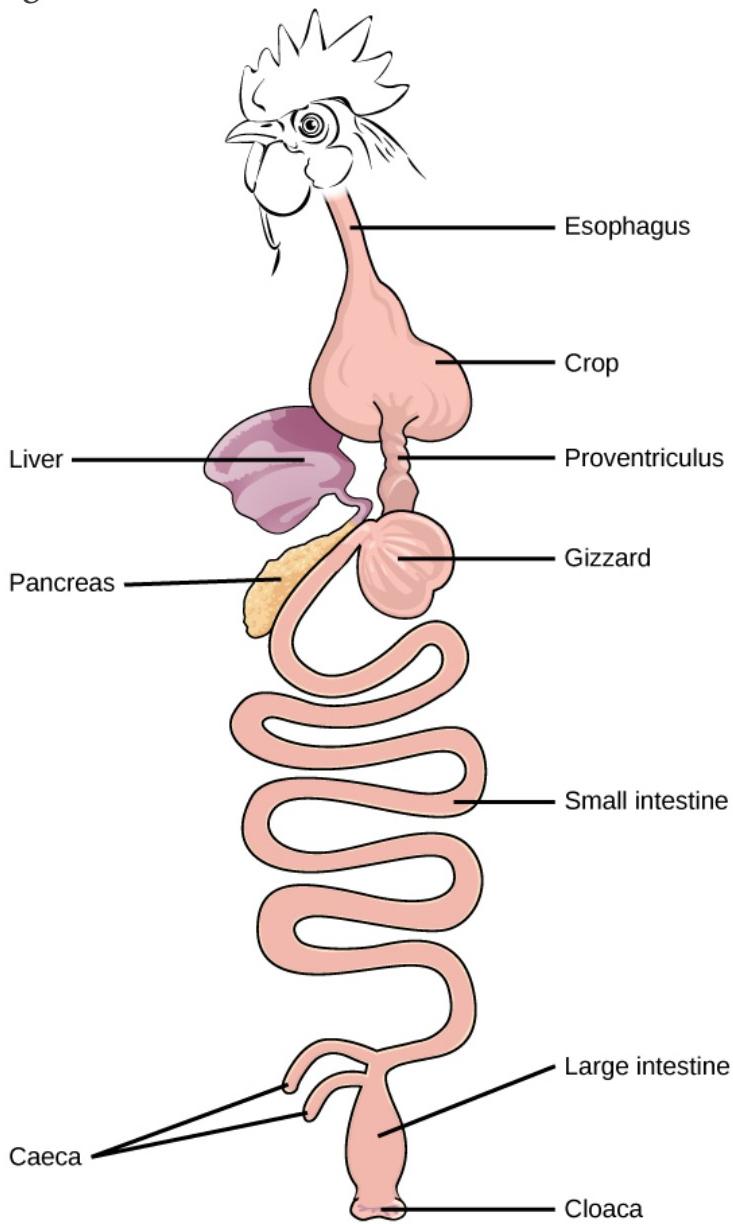


(b) Rabbit digestive system

Avian

Birds face special challenges when it comes to obtaining nutrition from food. They do not have teeth and so their digestive system, shown in [\[link\]](#), must be able to process un-masticated food. Birds have evolved a variety of beak types that reflect the vast variety in their diet, ranging from seeds and insects to fruits and nuts. Because most birds fly, their metabolic rates are high in order to efficiently process food and keep their body weight low. The stomach of birds has two chambers: the **proventriculus**, where gastric juices are produced to digest the food before it enters the stomach, and the **gizzard**, where the food is stored, soaked, and mechanically ground. The undigested material forms food pellets that are sometimes regurgitated.

Most of the chemical digestion and absorption happens in the intestine and the waste is excreted through the cloaca.



Evolution Connection

Avian Adaptations

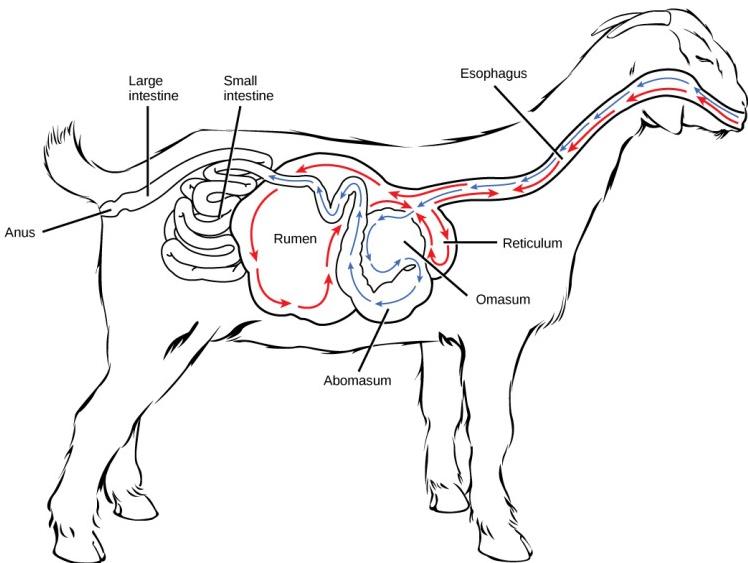
Birds have a highly efficient, simplified digestive system. Recent fossil evidence has shown that the evolutionary divergence of birds from other land animals was characterized by streamlining and simplifying the digestive system. Unlike many other animals, birds do not have teeth to chew their food. In place of lips, they have sharp pointy beaks. The horny beak, lack of jaws, and the smaller tongue of the birds can be traced back to their dinosaur ancestors. The emergence of these changes seems to coincide with the inclusion of seeds in the bird diet. Seed-eating birds have beaks that are shaped for grabbing seeds and the two-compartment stomach allows for delegation of tasks. Since birds need to remain light in order to fly, their metabolic rates are very high, which means they digest their food very quickly and need to eat often. Contrast this with the ruminants, where the digestion of plant matter takes a very long time.

Ruminants

Ruminants are mainly herbivores like cows, sheep, and goats, whose entire diet consists of eating large amounts of **roughage** or fiber. They have evolved digestive systems that help them digest vast

amounts of cellulose. An interesting feature of the ruminants' mouth is that they do not have upper incisor teeth. They use their lower teeth, tongue and lips to tear and chew their food. From the mouth, the food travels to the esophagus and on to the stomach.

To help digest the large amount of plant material, the stomach of the ruminants is a multi-chambered organ, as illustrated in [\[link\]](#). The four compartments of the stomach are called the rumen, reticulum, omasum, and abomasum. These chambers contain many microbes that breakdown cellulose and ferment ingested food. The abomasum is the “true” stomach and is the equivalent of the monogastric stomach chamber where gastric juices are secreted. The four-compartment gastric chamber provides larger space and the microbial support necessary to digest plant material in ruminants. The fermentation process produces large amounts of gas in the stomach chamber, which must be eliminated. As in other animals, the small intestine plays an important role in nutrient absorption, and the large intestine helps in the elimination of waste.



Pseudo-ruminants

Some animals, such as camels and alpacas, are pseudo-ruminants. They eat a lot of plant material and roughage. Digesting plant material is not easy because plant cell walls contain the polymeric sugar molecule cellulose. The digestive enzymes of these animals cannot breakdown cellulose, but microorganisms present in the digestive system can. Therefore, the digestive system must be able to handle large amounts of roughage and breakdown the cellulose. Pseudo-ruminants have a three-chamber stomach in the digestive system. However, their cecum—a pouched organ at the beginning of the large intestine containing many microorganisms that are necessary for the digestion of plant materials—is large and is the site where the

roughage is fermented and digested. These animals do not have a rumen but have an omasum, abomasum, and reticulum.

Digestion of food begins in the (a) oral cavity. Food is masticated by teeth and moistened by saliva secreted from the (b) salivary glands. Enzymes in the saliva begin to digest starches and fats. With the help of the tongue, the resulting bolus is moved into the esophagus by swallowing. (credit: modification of work by the National Cancer Institute) The esophagus transfers food from the mouth to the stomach through peristaltic movements. The large intestine reabsorbs water from undigested food and stores waste material until it is eliminated.

Parts of the Digestive System

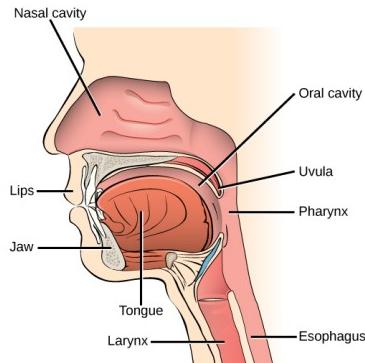
The vertebrate digestive system is designed to facilitate the transformation of food matter into the nutrient components that sustain organisms.

Oral Cavity

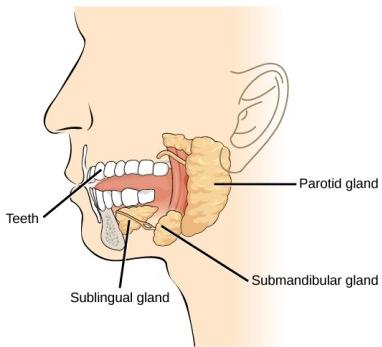
The oral cavity, or mouth, is the point of entry of food into the digestive system, illustrated in [\[link\]](#). The food consumed is broken into smaller particles by mastication, the chewing action of the teeth. All mammals have teeth and can chew their food.

The extensive chemical process of digestion begins

in the mouth. As food is being chewed, saliva, produced by the salivary glands, mixes with the food. Saliva is a watery substance produced in the mouths of many animals. There are three major glands that secrete saliva—the parotid, the submandibular, and the sublingual. Saliva contains mucus that moistens food and buffers the pH of the food. Saliva also contains immunoglobulins and lysozymes, which have antibacterial action to reduce tooth decay by inhibiting growth of some bacteria. Saliva also contains an enzyme called **salivary amylase** that begins the process of converting starches in the food into a disaccharide called maltose. Another enzyme called **lipase** is produced by the cells in the tongue. Lipases are a class of enzymes that can breakdown triglycerides. The lingual lipase begins the breakdown of fat components in the food. The chewing and wetting action provided by the teeth and saliva prepare the food into a mass called the **bolus** for swallowing. The tongue helps in swallowing—moving the bolus from the mouth into the pharynx. The pharynx opens to two passageways: the trachea, which leads to the lungs, and the esophagus, which leads to the stomach. The trachea has an opening called the glottis, which is covered by a cartilaginous flap called the epiglottis. When swallowing, the epiglottis closes the glottis and food passes into the esophagus and not the trachea. This arrangement allows food to be kept out of the trachea.



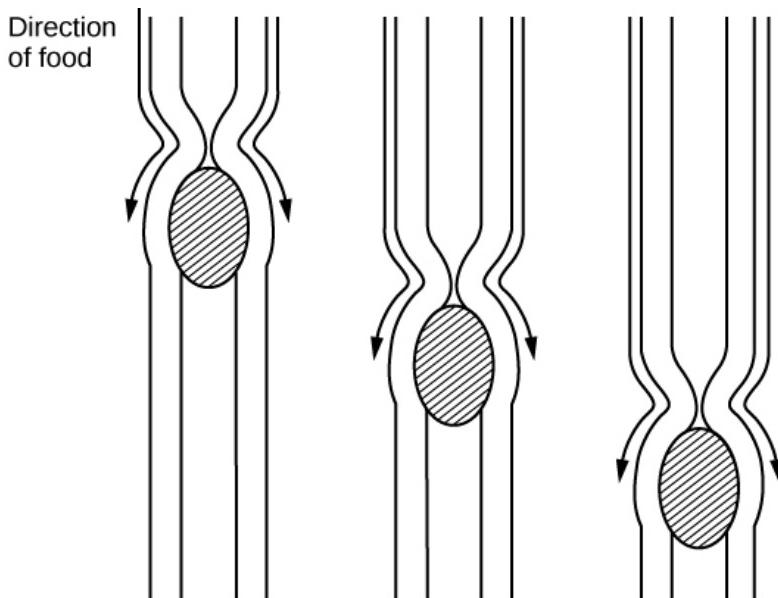
(a)



(b)

Esophagus

The **esophagus** is a tubular organ that connects the mouth to the stomach. The chewed and softened food passes through the esophagus after being swallowed. The smooth muscles of the esophagus undergo a series of wave like movements called **peristalsis** that push the food toward the stomach, as illustrated in [\[link\]](#). The peristalsis wave is unidirectional—it moves food from the mouth to the stomach, and reverse movement is not possible. The peristaltic movement of the esophagus is an involuntary reflex; it takes place in response to the act of swallowing.



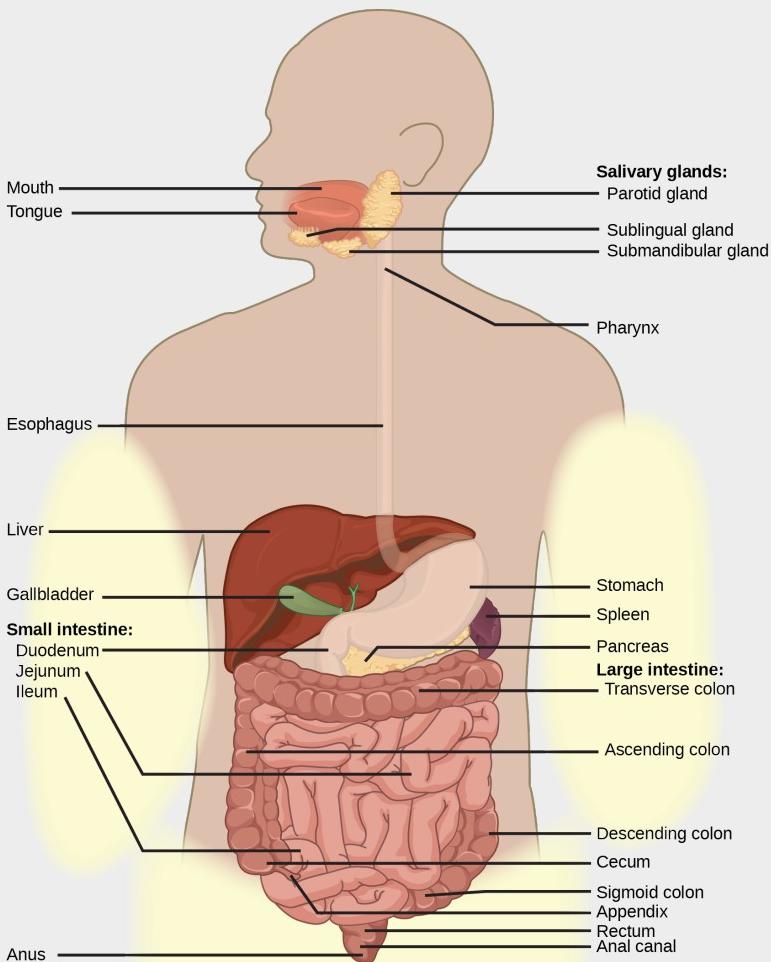
A ring-like muscle called a **sphincter** forms valves in the digestive system. The gastro-esophageal sphincter is located at the stomach end of the esophagus. In response to swallowing and the pressure exerted by the bolus of food, this sphincter opens, and the bolus enters the stomach. When there is no swallowing action, this sphincter is shut and prevents the contents of the stomach from traveling up the esophagus. Many animals have a true sphincter; however, in humans, there is no true sphincter, but the esophagus remains closed when there is no swallowing action. Acid reflux or “heartburn” occurs when the acidic digestive juices escape into the esophagus.

Stomach

A large part of digestion occurs in the stomach, shown in [\[link\]](#). The **stomach** is a saclike organ that secretes gastric digestive juices. The pH in the stomach is between 1.5 and 2.5. This highly acidic environment is required for the chemical breakdown of food and the extraction of nutrients. When empty, the stomach is a rather small organ; however, it can expand to up to 20 times its resting size when filled with food. This characteristic is particularly useful for animals that need to eat when food is available.

Visual Connection

The human stomach has an extremely acidic environment where most of the protein gets digested. (credit: modification of work by Mariana Ruiz Villareal)



Which of the following statements about the digestive system is false?

1. Chyme is a mixture of food and digestive

- juices that is produced in the stomach.
2. Food enters the large intestine before the small intestine.
 3. In the small intestine, chyme mixes with bile, which emulsifies fats.
 4. The stomach is separated from the small intestine by the pyloric sphincter.

The stomach is also the major site for protein digestion in animals other than ruminants. Protein digestion is mediated by an enzyme called pepsin in the stomach chamber. **Pepsin** is secreted by the chief cells in the stomach in an inactive form called **pepsinogen**. Pepsin breaks peptide bonds and cleaves proteins into smaller polypeptides; it also helps activate more pepsinogen, starting a positive feedback mechanism that generates more pepsin. Another cell type—parietal cells—secrete hydrogen and chloride ions, which combine in the lumen to form hydrochloric acid, the primary acidic component of the stomach juices. Hydrochloric acid helps to convert the inactive pepsinogen to pepsin. The highly acidic environment also kills many microorganisms in the food and, combined with the action of the enzyme pepsin, results in the hydrolysis of protein in the food. Chemical digestion is facilitated by the churning action of the stomach. Contraction and relaxation of smooth muscles mixes the stomach contents about every 20 minutes. The

partially digested food and gastric juice mixture is called **chyme**. Chyme passes from the stomach to the small intestine. Further protein digestion takes place in the small intestine. Gastric emptying occurs within two to six hours after a meal. Only a small amount of chyme is released into the small intestine at a time. The movement of chyme from the stomach into the small intestine is regulated by the pyloric sphincter.

When digesting protein and some fats, the stomach lining must be protected from getting digested by pepsin. There are two points to consider when describing how the stomach lining is protected. First, as previously mentioned, the enzyme pepsin is synthesized in the inactive form. This protects the chief cells, because pepsinogen does not have the same enzyme functionality of pepsin. Second, the stomach has a thick mucus lining that protects the underlying tissue from the action of the digestive juices. When this mucus lining is ruptured, ulcers can form in the stomach. Ulcers are open wounds in or on an organ caused by bacteria (*Helicobacter pylori*) when the mucus lining is ruptured and fails to reform.

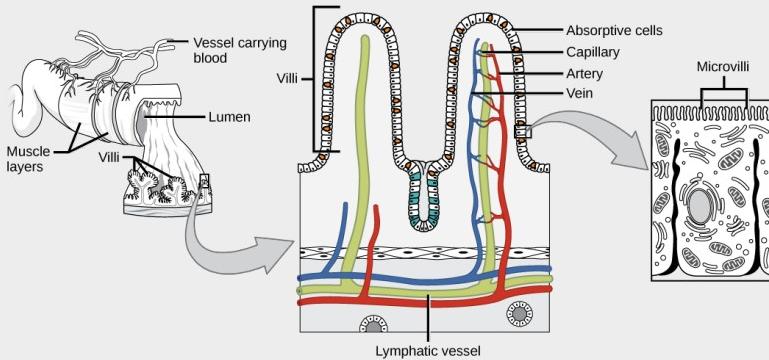
Small Intestine

Chyme moves from the stomach to the small intestine. The **small intestine** is the organ where the digestion of protein, fats, and carbohydrates is

completed. The small intestine is a long tube-like organ with a highly folded surface containing finger-like projections called the **villi**. The apical surface of each villus has many microscopic projections called microvilli. These structures, illustrated in [\[link\]](#), are lined with epithelial cells on the luminal side and allow for the nutrients to be absorbed from the digested food and absorbed into the bloodstream on the other side. The villi and microvilli, with their many folds, increase the surface area of the intestine and increase absorption efficiency of the nutrients. Absorbed nutrients in the blood are carried into the hepatic portal vein, which leads to the liver. There, the liver regulates the distribution of nutrients to the rest of the body and removes toxic substances, including drugs, alcohol, and some pathogens.

Visual Connection

Villi are folds on the small intestine lining that increase the surface area to facilitate the absorption of nutrients.



Which of the following statements about the small intestine is false?

1. Absorptive cells that line the small intestine have microvilli, small projections that increase surface area and aid in the absorption of food.
2. The inside of the small intestine has many folds, called villi.
3. Microvilli are lined with blood vessels as well as lymphatic vessels.
4. The inside of the small intestine is called the lumen.

The human small intestine is over 6m long and is divided into three parts: the duodenum, the jejunum, and the ileum. The “C-shaped,” fixed part of the small intestine is called the **duodenum** and is shown in [\[link\]](#). The duodenum is separated from the stomach by the pyloric sphincter which opens to allow chyme to move from the stomach to the duodenum. In the duodenum, chyme is mixed with

pancreatic juices in an alkaline solution rich in bicarbonate that neutralizes the acidity of chyme and acts as a buffer. Pancreatic juices also contain several digestive enzymes. Digestive juices from the pancreas, liver, and gallbladder, as well as from gland cells of the intestinal wall itself, enter the duodenum. **Bile** is produced in the liver and stored and concentrated in the gallbladder. Bile contains bile salts which emulsify lipids while the pancreas produces enzymes that catabolize starches, disaccharides, proteins, and fats. These digestive juices breakdown the food particles in the chyme into glucose, triglycerides, and amino acids. Some chemical digestion of food takes place in the duodenum. Absorption of fatty acids also takes place in the duodenum.

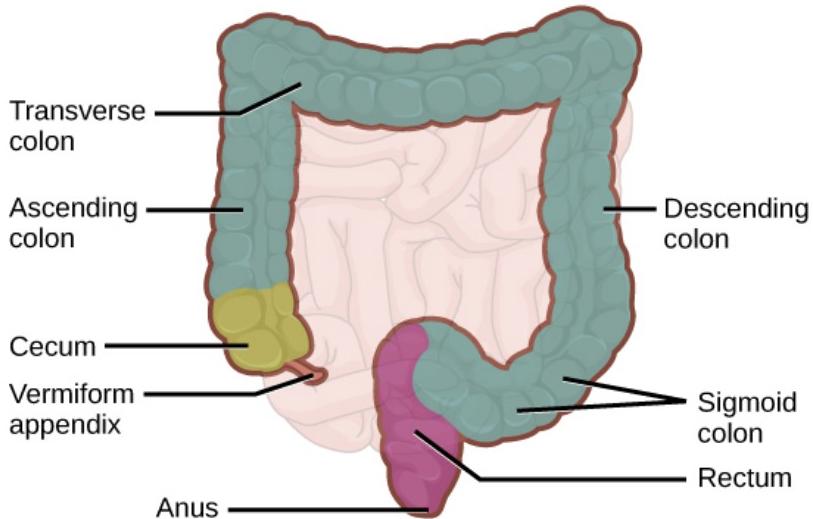
The second part of the small intestine is called the **jejunum**, shown in [\[link\]](#). Here, hydrolysis of nutrients is continued while most of the carbohydrates and amino acids are absorbed through the intestinal lining. The bulk of chemical digestion and nutrient absorption occurs in the jejunum.

The **ileum**, also illustrated in [\[link\]](#) is the last part of the small intestine and here the bile salts and vitamins are absorbed into the bloodstream. The undigested food is sent to the colon from the ileum via peristaltic movements of the muscle. The ileum ends and the large intestine begins at the ileocecal

valve. The vermiform, “worm-like,” appendix is located at the ileocecal valve. The appendix of humans secretes no enzymes and has an insignificant role in immunity.

Large Intestine

The **large intestine**, illustrated in [\[link\]](#), reabsorbs the water from the undigested food material and processes the waste material. The human large intestine is much smaller in length compared to the small intestine but larger in diameter. It has three parts: the cecum, the colon, and the rectum. The cecum joins the ileum to the colon and is the receiving pouch for the waste matter. The colon is home to many bacteria or “intestinal flora” that aid in the digestive processes. The colon can be divided into four regions, the ascending colon, the transverse colon, the descending colon, and the sigmoid colon. The main functions of the colon are to extract the water and mineral salts from undigested food, and to store waste material. Carnivorous mammals have a shorter large intestine compared to herbivorous mammals due to their diet.



Rectum and Anus

The **rectum** is the terminal end of the large intestine, as shown in [\[link\]](#). The primary role of the rectum is to store the feces until defecation. The feces are propelled using peristaltic movements during elimination. The **anus** is an opening at the far-end of the digestive tract and is the exit point for the waste material. Two sphincters between the rectum and anus control elimination: the inner sphincter is involuntary and the outer sphincter is voluntary.

Accessory Organs

The organs discussed above are the organs of the digestive tract through which food passes. Accessory organs are organs that add secretions (enzymes) that

catabolize food into nutrients. Accessory organs include salivary glands, the liver, the pancreas, and the gallbladder. The liver, pancreas, and gallbladder are regulated by hormones in response to the food consumed.

The **liver** is the largest internal organ in humans and it plays a very important role in digestion of fats and detoxifying blood. The liver produces bile, a digestive juice that is required for the breakdown of fatty components of the food in the duodenum. The liver also processes the vitamins and fats and synthesizes many plasma proteins.

The **pancreas** is another important gland that secretes digestive juices. The chyme produced from the stomach is highly acidic in nature; the pancreatic juices contain high levels of bicarbonate, an alkali that neutralizes the acidic chyme. Additionally, the pancreatic juices contain a large variety of enzymes that are required for the digestion of protein and carbohydrates.

The **gallbladder** is a small organ that aids the liver by storing bile and concentrating bile salts. When chyme containing fatty acids enters the duodenum, the bile is secreted from the gallbladder into the duodenum.

Section Summary

Different animals have evolved different types of digestive systems specialized to meet their dietary needs. Humans and many other animals have monogastric digestive systems with a single-chambered stomach. Birds have evolved a digestive system that includes a gizzard where the food is crushed into smaller pieces. This compensates for their inability to masticate. Ruminants that consume large amounts of plant material have a multi-chambered stomach that digests roughage. Pseudo-ruminants have similar digestive processes as ruminants but do not have the four-compartment stomach. Processing food involves ingestion (eating), digestion (mechanical and enzymatic breakdown of large molecules), absorption (cellular uptake of nutrients), and elimination (removal of undigested waste as feces).

Many organs work together to digest food and absorb nutrients. The mouth is the point of ingestion and the location where both mechanical and chemical breakdown of food begins. Saliva contains an enzyme called amylase that breaks down carbohydrates. The food bolus travels through the esophagus by peristaltic movements to the stomach. The stomach has an extremely acidic environment. An enzyme called pepsin digests protein in the stomach. Further digestion and absorption take place in the small intestine. The large intestine reabsorbs water from the undigested food and stores waste until elimination.

Visual Connection Questions

[\[link\]](#) Which of the following statements about the digestive system is false?

1. Chyme is a mixture of food and digestive juices that is produced in the stomach.
2. Food enters the large intestine before the small intestine.
3. In the small intestine, chyme mixes with bile, which emulsifies fats.
4. The stomach is separated from the small intestine by the pyloric sphincter.

[\[link\]](#) B

[\[link\]](#) Which of the following statements about the small intestine is false?

1. Absorptive cells that line the small intestine have microvilli, small projections that increase surface area and aid in the absorption of food.
2. The inside of the small intestine has many folds, called villi.
3. Microvilli are lined with blood vessels as

well as lymphatic vessels.

4. The inside of the small intestine is called the lumen.
-

[\[link\]](#) C

Review Questions

Which of the following is a pseudo-ruminant?

1. cow
 2. pig
 3. crow
 4. horse
-

D

Which of the following statements is untrue?

1. Roughage takes a long time to digest.
2. Birds eat large quantities at one time so that they can fly long distances.
3. Cows do not have upper teeth.
4. In pseudo-ruminants, roughage is digested in the cecum.

B

The acidic nature of chyme is neutralized by

_____.

1. potassium hydroxide
 2. sodium hydroxide
 3. bicarbonates
 4. vinegar
-

C

The digestive juices from the liver are delivered to the _____.

1. stomach
 2. liver
 3. duodenum
 4. colon
-

C

A scientist dissects a new species of animal. If the animal's digestive system has a single stomach with an extended small intestine, to which animal could the dissected specimen be closely related?

1. lion
 2. snowshoe hare
 3. earthworm
 4. eagle
-

B

Critical Thinking Questions

How does the polygastric digestive system aid in digesting roughage?

Animals with a polygastric digestive system have a multi-chambered stomach. The four compartments of the stomach are called the rumen, reticulum, omasum, and abomasum. These chambers contain many microbes that breakdown the cellulose and ferment the ingested food. The abomasum is the “true” stomach and is the equivalent of a monogastric stomach chamber where gastric juices are secreted. The four-compartment gastric chamber provides larger space and the microbial support necessary for ruminants to digest plant material.

How do birds digest their food in the absence of teeth?

Birds have a stomach chamber called a gizzard. Here, the food is stored, soaked, and ground into finer particles, often using pebbles. Once this process is complete, the digestive juices take over in the proventriculus and continue the digestive process.

What is the role of the accessory organs in digestion?

Accessory organs play an important role in producing and delivering digestive juices to the intestine during digestion and absorption. Specifically, the salivary glands, liver, pancreas, and gallbladder play important roles. Malfunction of any of these organs can lead to disease states.

Explain how the villi and microvilli aid in absorption.

The villi and microvilli are folds on the surface of the small intestine. These folds increase the surface area of the intestine and provide more

area for the absorption of nutrients.

Name two components of the digestive system that perform mechanical digestion. Describe how mechanical digestion contributes to acquiring nutrients from food.

The stomach and the teeth both perform mechanical digestion, which is physically (as opposed to chemically) breaking the food into smaller components. This exposes a larger surface area for chemical digestion and release of nutrients. The teeth are vital to mastication, which breaks large bites of food down into smaller pieces that are easily swallowed. The stomach's muscle contractions churn the food to expose all particles to the acid and digestive enzymes.

Glossary

alimentary canal

tubular digestive system with a mouth and anus

anus

exit point for waste material

bile

digestive juice produced by the liver;
important for digestion of lipids

bolus

mass of food resulting from chewing action
and wetting by saliva

carnivore

animal that consumes animal flesh

chyme

mixture of partially digested food and
stomach juices

duodenum

first part of the small intestine where a large
part of digestion of carbohydrates and fats
occurs

esophagus

tubular organ that connects the mouth to the
stomach

gallbladder

organ that stores and concentrates bile

gastrovascular cavity

digestive system consisting of a single
opening

gizzard

muscular organ that grinds food

herbivore

animal that consumes a strictly plant diet

ileum

last part of the small intestine; connects the small intestine to the large intestine;
important for absorption of B-12

jejunum

second part of the small intestine

large intestine

digestive system organ that reabsorbs water from undigested material and processes waste matter

lipase

enzyme that chemically breaks down lipids

liver

organ that produces bile for digestion and processes vitamins and lipids

monogastric

digestive system that consists of a single-chambered stomach

omnivore

animal that consumes both plants and animals

pancreas

gland that secretes digestive juices

pepsin

enzyme found in the stomach whose main role is protein digestion

pepsinogen

inactive form of pepsin

peristalsis

wave-like movements of muscle tissue

proventriculus

glandular part of a bird's stomach

rectum

area of the body where feces is stored until elimination

roughage

component of food that is low in energy and high in fiber

ruminant

animal with a stomach divided into four compartments

salivary amylase

enzyme found in saliva, which converts carbohydrates to maltose

small intestine

organ where digestion of protein, fats, and carbohydrates is completed

sphincter

band of muscle that controls movement of materials throughout the digestive tract

stomach

saclike organ containing acidic digestive juices

villi

folds on the inner surface of the small intestine whose role is to increase absorption area

Nutrition and Energy Production

By the end of this section, you will be able to do the following:

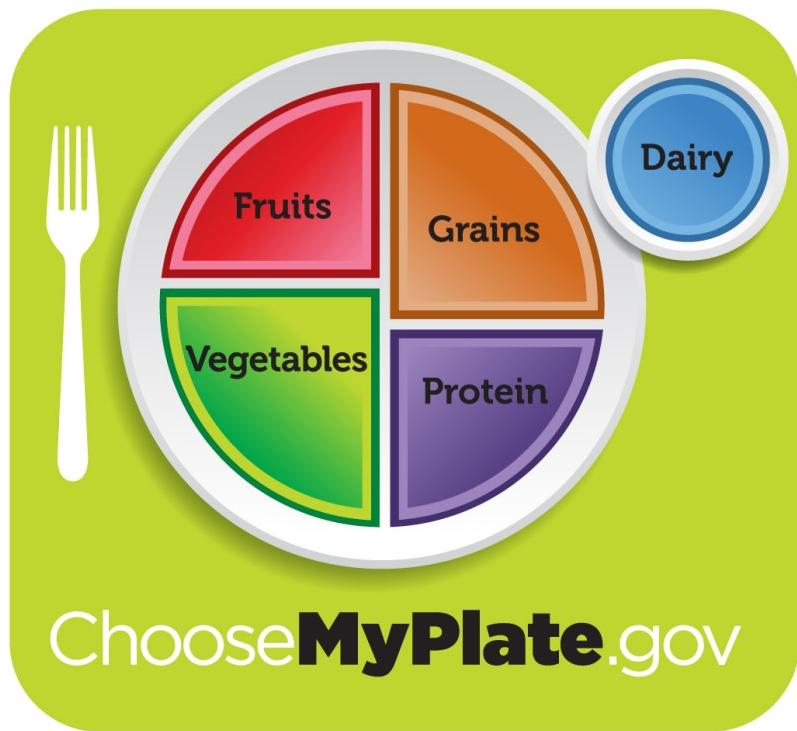
- Explain why an animal's diet should be balanced and meet the needs of the body
- Define the primary components of food
- Describe the essential nutrients required for cellular function that cannot be synthesized by the animal body
- Explain how energy is produced through diet and digestion
- Describe how excess carbohydrates and energy are stored in the body

Given the diversity of animal life on our planet, it is not surprising that the animal diet would also vary substantially. The animal diet is the source of materials needed for building DNA and other complex molecules needed for growth, maintenance, and reproduction; collectively these processes are called biosynthesis. The diet is also the source of materials for ATP production in the cells. The diet must be balanced to provide the minerals and vitamins that are required for cellular function.

For humans, a balanced diet includes fruits, vegetables, grains, and protein. (credit: USDA) A healthy diet should include a variety of foods to ensure that needs for essential nutrients are met. (credit: Keith Weller, USDA ARS)

Food Requirements

What are the fundamental requirements of the animal diet? The animal diet should be well balanced and provide nutrients required for bodily function and the minerals and vitamins required for maintaining structure and regulation necessary for good health and reproductive capability. These requirements for a human are illustrated graphically in [\[link\]](#)



Link to Learning

The first step in ensuring that you are meeting the

food requirements of your body is an awareness of the food groups and the nutrients they provide. To learn more about each food group and the recommended daily amounts, explore this [interactive site](#) by the United States Department of Agriculture.

Everyday Connection Let's Move! Campaign

Obesity is a growing epidemic and the rate of obesity among children is rapidly rising in the United States. To combat childhood obesity and ensure that children get a healthy start in life, first lady Michelle Obama has launched the Let's Move! campaign. The goal of this campaign is to educate parents and caregivers on providing healthy nutrition and encouraging active lifestyles to future generations. This program aims to involve the entire community, including parents, teachers, and healthcare providers to ensure that children have access to healthy foods—more fruits, vegetables, and whole grains—and consume fewer calories from processed foods. Another goal is to ensure that children get physical activity. With the increase in television viewing and stationary pursuits such as video games, sedentary lifestyles have become the norm. Learn more at <https://letsmove.obamawhitehouse.archives.gov>.

Organic Precursors

The organic molecules required for building cellular material and tissues must come from food.

Carbohydrates or sugars are the primary source of organic carbons in the animal body. During digestion, digestible carbohydrates are ultimately broken down into glucose and used to provide energy through metabolic pathways. Complex carbohydrates, including polysaccharides, can be broken down into glucose through biochemical modification; however, humans do not produce the enzyme cellulase and lack the ability to derive glucose from the polysaccharide cellulose. In humans, these molecules provide the fiber required for moving waste through the large intestine and a healthy colon. The intestinal flora in the human gut are able to extract some nutrition from these plant fibers. The excess sugars in the body are converted into glycogen and stored in the liver and muscles for later use. Glycogen stores are used to fuel prolonged exertions, such as long-distance running, and to provide energy during food shortage. Excess glycogen can be converted to fats, which are stored in the lower layer of the skin of mammals for insulation and energy storage. Excess digestible carbohydrates are stored by mammals in order to survive famine and aid in mobility.

Another important requirement is that of nitrogen. Protein catabolism provides a source of organic

nitrogen. Amino acids are the building blocks of proteins and protein breakdown provides amino acids that are used for cellular function. The carbon and nitrogen derived from these become the building block for nucleotides, nucleic acids, proteins, cells, and tissues. Excess nitrogen must be excreted as it is toxic. Fats add flavor to food and promote a sense of satiety or fullness. Fatty foods are also significant sources of energy because one gram of fat contains nine calories. Fats are required in the diet to aid the absorption of fat-soluble vitamins and the production of fat-soluble hormones.

Essential Nutrients

While the animal body can synthesize many of the molecules required for function from the organic precursors, there are some nutrients that need to be consumed from food. These nutrients are termed **essential nutrients**, meaning they must be eaten, and the body cannot produce them.

The omega-3 alpha-linolenic acid and the omega-6 linoleic acid are essential fatty acids needed to make some membrane phospholipids. **Vitamins** are another class of essential organic molecules that are required in small quantities for many enzymes to function and, for this reason, are considered to be coenzymes. Absence or low levels of vitamins can have a dramatic effect on health, as outlined in

[link] and [link]. Both fat-soluble and water-soluble vitamins must be obtained from food. Minerals, listed in [link], are inorganic essential nutrients that must be obtained from food. Among their many functions, minerals help in structure and regulation and are considered cofactors. Certain amino acids also must be procured from food and cannot be synthesized by the body. These amino acids are the “essential” amino acids. The human body can synthesize only 11 of the 20 required amino acids; the rest must be obtained from food. The essential amino acids are listed in [link].

Water-soluble Essential Vitamins

Vitamin	Function	Deficiencies Can Lead To	Sources
Vitamin B ₁ (Thiamine)	Needed by the body to process lipids, proteins, and heart carbohydrate function, coenzyme removes CO ₂ problems	Muscle weakness, Beriberi: reduced function, CNS problems	Milk, meat, dried beans, whole grains

from organic
compounds

Vitamin B ₂ (Riboflavin)	Takes an active role in metabolism, aiding in the conversion of food to energy (FAD and FMN)	Cracks or sores on the outer surface of the lips (cheliosis); inflammation and redness of the tongue; moist, scaly skin inflammation (seborrheic dermatitis)	Meat, eggs, enriched grains, vegetables
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Vitamin B ₃ (Niacin)	Used by the body to release energy from carbohydrates and to process alcohol; required for the synthesis of sex hormones; component of coenzyme NAD ⁺ and	Pellagra, which can result in dermatitis, diarrhea, dementia, and death	Meat, eggs, grains, nuts, potatoes
------------------------------------	--	---	------------------------------------

NADP +

Vitamin B ₅ (Pantothenic acid)	Assists in producing energy from foods (lipids, retarded in particular) component of coenzyme A	Fatigue, poor coordination, retarded growth, numbness, tingling of hands and feet	Meat, whole grains, milk, fruits, vegetables
Vitamin B ₆ (Pyridoxine)	The principal vitamin for processing amino acids and lipids; also helps convert nutrients into energy	Irritability, depression, confusion, mouth sores or ulcers, anemia, muscular twitching	Meat, dairy products, whole grains, orange juice
Vitamin B ₇ (Biotin)	Used in energy and amino acid metabolism, fat synthesis, and fat breakdown; helps the body use blood sugar	Hair loss, dermatitis, depression, numbness in the extremities; neuromuscular disorders	Meat, eggs, legumes and other vegetables
Vitamin B ₉	Assists the	Deficiency	Leafy green

(Folic acid) normal development during pregnancy is whole of cells, associated especially with birth during fetal defects, such as neural development; helps tube defects metabolize and anemia nucleic and amino acids

Vitamin B12 (Cobalamin) Maintains healthy nervous system and assists with blood cell formation; coenzyme in nucleic acid metabolism

Anemia, neurological disorders, numbness, loss of balance

Meat, eggs, animal products

Vitamin C (Ascorbic acid)

Helps maintain connective tissue: bone, cartilage, and dentin; boosts the immune system

Scurvy, which results in bleeding, hair and tooth loss; joint pain and swelling; delayed wound

Citrus fruits, broccoli, tomatoes, red sweet bell peppers

healing

Fat-soluble Essential Vitamins

Vitamin	Function	Deficiencies Can Lead To	Sources
Vitamin A (Retinol)	Critical to the development of bones, teeth, and skin; helps maintain eyesight, enhances the immune system, fetal development, gene expression	Night-blindness, skin disorders, impaired immunity	Dark green leafy vegetables, yellow-orange vegetables, fruits, milk, butter
Vitamin D	Critical for calcium absorption for bone development and strength;	Rickets, osteomalacia, immunity	Cod liver oil, milk, egg yolk

maintains a stable nervous system; maintains a normal and strong heartbeat; helps in blood clotting

Vitamin E (Tocopherol) Lessens oxidative damage of cells and prevents lung damage from pollutants; vital to the immune system

Deficiency is rare; anemia, nervous system degeneration

Wheat germ oil, unrefined vegetable oils, nuts, seeds, grains

Vitamin K (Phylloquinone) Essential to blood clotting

Bleeding and easy bruising

Leafy green vegetables, tea



Minerals and Their Function in the Human Body

Mineral	Function	Deficiencies	Sources
*Calcium	Needed for muscle and neuron function; heart health; impaired builds bone growth and supports	Osteoporosis, rickets, muscle spasms, growth	Milk, yogurt, fish, green leafy vegetables, legumes

synthesis
and function
of blood
cells; nerve
function

*Chlorine

Needed for production of hydrochloric acid (HCl) in reduced the stomach appetite and nerve function; osmotic balance

Muscle cramps, mood

Table salt

Copper (trace amounts)

Required component of many redox enzymes, including cytochrome c oxidase; cofactor for hemoglobin synthesis

Copper deficiency is rare

Liver, oysters, cocoa, chocolate, sesame, nuts

Iodine

Required for Goiter the synthesis of thyroid hormones

Seafood, iodized salt, dairy products

Iron

Required for Anemia,

Red meat,

	many proteins and enzymes, notably hemoglobin, poor to prevent anemia	which causes fatigue, and anemia	leafy green vegetables, concentration of fish (tuna, salmon), eggs, dried fruits, beans, whole grains
*Magnesium	Required cofactor for ATP formation; bone formation; normal membrane functions; muscle function	Mood disturbances, muscle spasms	Whole grains, leafy green vegetables
Manganese (trace amounts)	A cofactor in enzyme functions; trace amounts are required	Manganese deficiency is rare	Common in most foods
Molybdenum (trace amounts)	Acts as a cofactor for three essential enzymes in humans: sulfite	Molybdenum deficiency is rare	

oxidase,
xanthine
oxidase, and
aldehyde
oxidase

*Phosphorus A

Weakness, component bone of bones and abnormalities whole teeth; helps regulate acid-base balance; nucleotide synthesis

*Potassium

Vital for muscles, heart, and nerve function

Cardiac rhythm disturbance, muscle weakness

Legumes, potato skin, tomatoes, bananas

Selenium (trace amounts)

A cofactor essential to activity of antioxidant enzymes like glutathione peroxidase; trace amounts are required

Selenium deficiency is rare

Common in most foods

*Sodium

Systemic electrolyte

Muscle cramps,

Table salt

required for fatigue,
many reduced
functions; appetite
acid-base
balance;
water
balance;
nerve
function

Zinc (trace amounts)

Required for Anemia, several poor wound healing, can lead to short stature
enzymes such as carboxypeptidase, liver alcohol dehydrogenase, and carbonic anhydrase

*Greater than 200mg/day required

Common in most foods

Essential Amino Acids

Amino acids that must be consumed
isoleucine
leucine

Amino acids anabolized by the body
alanine
selenocysteine

lysine	aspartate
methionine	cysteine
phenylalanine	glutamate
tryptophan	glycine
valine	proline
histidine*	serine
threonine	tyrosine
arginine*	asparagine

*The human body can synthesize histidine and arginine, but not in the quantities required, especially for growing children.

Food Energy and ATP

Animals need food to obtain energy and maintain homeostasis. Homeostasis is the ability of a system to maintain a stable internal environment even in the face of external changes to the environment. For example, the normal body temperature of humans is 37°C (98.6°F). Humans maintain this temperature even when the external temperature is hot or cold. It takes energy to maintain this body temperature, and animals obtain this energy from food.

The primary source of energy for animals is carbohydrates, mainly glucose. Glucose is called the

body's fuel. The digestible carbohydrates in an animal's diet are converted to glucose molecules through a series of catabolic chemical reactions.

Adenosine triphosphate, or ATP, is the primary energy currency in cells; ATP stores energy in phosphate ester bonds. ATP releases energy when the phosphodiester bonds are broken and ATP is converted to ADP and a phosphate group. ATP is produced by the oxidative reactions in the cytoplasm and mitochondrion of the cell, where carbohydrates, proteins, and fats undergo a series of metabolic reactions collectively called cellular respiration. For example, glycolysis is a series of reactions in which glucose is converted to pyruvic acid and some of its chemical potential energy is transferred to NADH and ATP.

ATP is required for all cellular functions. It is used to build the organic molecules that are required for cells and tissues; it provides energy for muscle contraction and for the transmission of electrical signals in the nervous system. When the amount of ATP is available in excess of the body's requirements, the liver uses the excess ATP and excess glucose to produce molecules called glycogen. Glycogen is a polymeric form of glucose and is stored in the liver and skeletal muscle cells. When blood sugar drops, the liver releases glucose from stores of glycogen. Skeletal muscle converts glycogen to glucose during intense exercise. The

process of converting glucose and excess ATP to glycogen and the storage of excess energy is an evolutionarily important step in helping animals deal with mobility, food shortages, and famine.

Everyday Connection

Obesity

Obesity is a major health concern in the United States, and there is a growing focus on reducing obesity and the diseases it may lead to, such as type-2 diabetes, cancers of the colon and breast, and cardiovascular disease. How does the food consumed contribute to obesity?

Fatty foods are calorie-dense, meaning that they have more calories per unit mass than carbohydrates or proteins. One gram of carbohydrates has four calories, one gram of protein has four calories, and one gram of fat has nine calories. Animals tend to seek lipid-rich food for their higher energy content.

The signals of hunger (“time to eat”) and satiety (“time to stop eating”) are controlled in the hypothalamus region of the brain. Foods that are rich in fatty acids tend to promote satiety more than foods that are rich only in carbohydrates.

Excess carbohydrate and ATP are used by the liver to synthesize glycogen. The pyruvate produced during glycolysis is used to synthesize fatty acids. When there is more glucose in the body than

required, the resulting excess pyruvate is converted into molecules that eventually result in the synthesis of fatty acids within the body. These fatty acids are stored in adipose cells—the fat cells in the mammalian body whose primary role is to store fat for later use.

It is important to note that some animals benefit from obesity. Polar bears and seals need body fat for insulation and to keep them from losing body heat during Arctic winters. When food is scarce, stored body fat provides energy for maintaining homeostasis. Fats prevent famine in mammals, allowing them to access energy when food is not available on a daily basis; fats are stored when a large kill is made or lots of food is available.

Section Summary

Animal diet should be balanced and meet the needs of the body. Carbohydrates, proteins, and fats are the primary components of food. Some essential nutrients are required for cellular function but cannot be produced by the animal body. These include vitamins, minerals, some fatty acids, and some amino acids. Food intake in more than necessary amounts is stored as glycogen in the liver and muscle cells, and in fat cells. Excess adipose

storage can lead to obesity and serious health problems. ATP is the energy currency of the cell and is obtained from the metabolic pathways. Excess carbohydrates and energy are stored as glycogen in the body.

Review Questions

Which of the following statements is not true?

1. Essential nutrients can be synthesized by the body.
2. Vitamins are required in small quantities for bodily function.
3. Some amino acids can be synthesized by the body, while others need to be obtained from diet.
4. Vitamins come in two categories: fat-soluble and water-soluble.

A

Which of the following is a water-soluble vitamin?

1. vitamin A
2. vitamin E

-
- 3. vitamin K
 - 4. vitamin C
-

D

What is the primary fuel for the body?

- 1. carbohydrates
 - 2. lipids
 - 3. protein
 - 4. glycogen
-

A

Excess glucose is stored as _____.

- 1. fat
 - 2. glucagon
 - 3. glycogen
 - 4. it is not stored in the body
-

C

Many distance runners “carb load” the day before a big race. How does this eating strategy provide an advantage to the runner?

-
1. The carbohydrates cause the release of insulin.
 2. The excess carbohydrates are converted to fats, which have a higher calorie density.
 3. The glucose from the carbohydrates lets the muscles make excess ATP overnight.
 4. The excess carbohydrates can be stored in the muscles as glycogen.

D

Critical Thinking Questions

What are essential nutrients?

Essential nutrients are those nutrients that must be obtained from the diet because they cannot be produced by the body. Vitamins and minerals are examples of essential nutrients.

What is the role of minerals in maintaining good health?

Minerals—such as potassium, sodium, and calcium—are required for the functioning of

many cellular processes, including muscle contraction and nerve conduction. While minerals are required in trace amounts, not having minerals in the diet can be potentially harmful.

Discuss why obesity is a growing epidemic.

In the United States, obesity, particularly childhood obesity, is a growing concern. Some of the contributors to this situation include sedentary lifestyles and consuming more processed foods and less fruits and vegetables. As a result, even young children who are obese can face health concerns.

There are several nations where malnourishment is a common occurrence. What may be some of the health challenges posed by malnutrition?

Malnutrition, often in the form of not getting enough calories or not enough of the essential nutrients, can have severe consequences. Many malnourished children have vision and dental problems, and over the years may develop many serious health problems.

Generally describe how a piece of bread can power your legs as you walk up a flight of stairs.

A piece of bread is eaten and converted into chemical energy. The bread is broken down in the mouth by mastication and salivary enzymes, then transferred to the stomach for further digestion. After digestion by the acid and digestive enzymes in the stomach, the macromolecules that made up the bread move into the small intestine. In the small intestine, the carbohydrates from the bread are absorbed through the microvilli into the bloodstream. In muscle cells in the legs, the carbohydrates can be broken down into glucose, and then used for cellular respiration to create ATP. The muscles in the leg then use the ATP to perform the mechanical work needed to climb a flight of stairs.

In the 1990s fat-free foods became popular among people trying to lose weight. However, many dieticians now conclude that the fat-free trend made people less healthy and heavier. Describe how this could occur.

Fats are an essential component of a healthy diet, and needed by the body to function. Fats

are essential for many processes, including the absorption of fat-soluble vitamins and production of some hormones. Fats also send a satiation signal to the brain that regulates hunger. Without fats in their diets many people may have actually consumed more calories, which would have resulted in weight gain.

Glossary

essential nutrient

nutrient that cannot be synthesized by the body; it must be obtained from food

mineral

inorganic, elemental molecule that carries out important roles in the body

vitamin

organic substance necessary in small amounts to sustain life

Digestive System Processes

By the end of this section, you will be able to do the following:

- Describe the process of digestion
- Detail the steps involved in digestion and absorption
- Define elimination
- Explain the role of both the small and large intestines in absorption

Obtaining nutrition and energy from food is a multistep process. For true animals, the first step is ingestion, the act of taking in food. This is followed by digestion, absorption, and elimination. In the following sections, each of these steps will be discussed in detail.

Ingestion

The large molecules found in intact food cannot pass through the cell membranes. Food needs to be broken into smaller particles so that animals can harness the nutrients and organic molecules. The first step in this process is **ingestion**. Ingestion is the process of taking in food through the mouth. In vertebrates, the teeth, saliva, and tongue play important roles in mastication (preparing the food into bolus). While the food is being mechanically

broken down, the enzymes in saliva begin to chemically process the food as well. The combined action of these processes modifies the food from large particles to a soft mass that can be swallowed and can travel the length of the esophagus.

Digestion of carbohydrates is performed by several enzymes. Starch and glycogen are broken down into glucose by amylase and maltase. Sucrose (table sugar) and lactose (milk sugar) are broken down by sucrase and lactase, respectively. Protein digestion is a multistep process that begins in the stomach and continues through the intestines. Lipids are digested and absorbed in the small intestine.

Digestion and Absorption

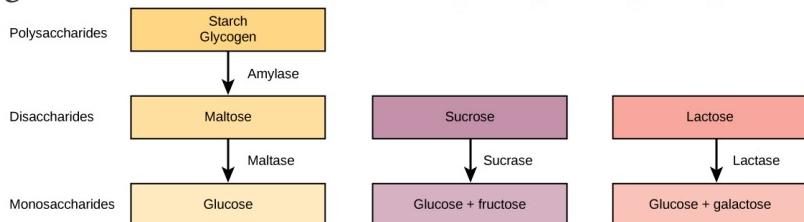
Digestion is the mechanical and chemical breakdown of food into small organic fragments. It is important to breakdown macromolecules into smaller fragments that are of suitable size for absorption across the digestive epithelium. Large, complex molecules of proteins, polysaccharides, and lipids must be reduced to simpler particles such as simple sugar before they can be absorbed by the digestive epithelial cells. Different organs play specific roles in the digestive process. The animal diet needs carbohydrates, protein, and fat, as well as vitamins and inorganic components for nutritional balance. How each of these components is digested is discussed in the following sections.

Carbohydrates

The digestion of carbohydrates begins in the mouth. The salivary enzyme amylase begins the breakdown of food starches into maltose, a disaccharide. As the bolus of food travels through the esophagus to the stomach, no significant digestion of carbohydrates takes place. The esophagus produces no digestive enzymes but does produce mucous for lubrication. The acidic environment in the stomach stops the action of the amylase enzyme.

The next step of carbohydrate digestion takes place in the duodenum. Recall that the chyme from the stomach enters the duodenum and mixes with the digestive secretion from the pancreas, liver, and gallbladder. Pancreatic juices also contain amylase, which continues the breakdown of starch and glycogen into maltose, a disaccharide. The disaccharides are broken down into monosaccharides by enzymes called **maltases**, **sucrases**, and **lactases**, which are also present in the brush border of the small intestinal wall. Maltase breaks down maltose into glucose. Other disaccharides, such as sucrose and lactose are broken down by sucrase and lactase, respectively. Sucrase breaks down sucrose (or “table sugar”) into glucose and fructose, and lactase breaks down lactose (or “milk sugar”) into glucose and galactose. The monosaccharides (glucose) thus produced are absorbed and then can be used in metabolic

pathways to harness energy. The monosaccharides are transported across the intestinal epithelium into the bloodstream to be transported to the different cells in the body. The steps in carbohydrate digestion are summarized in [link] and [link].

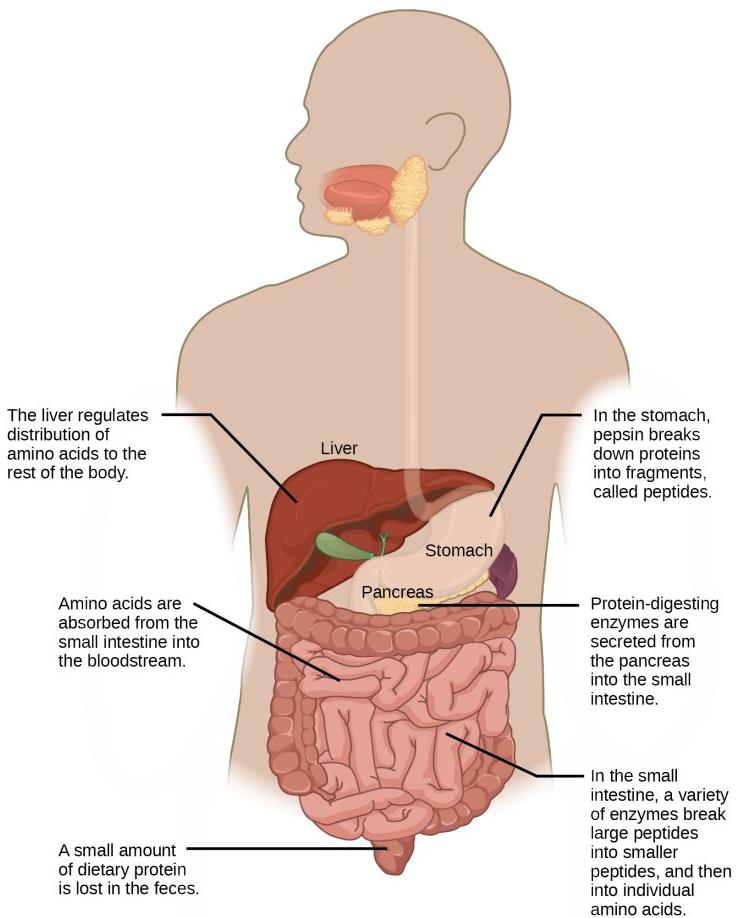


Digestion of Carbohydrates

Enzyme	Produced By	Site of Action	Substrate Acting On	End Products
Salivary amylase	Salivary glands	Mouth	Polysaccharides (Starch)	Disaccharides (maltose), oligosaccharides
Pancreatic amylase	Pancreas	Small intestine	Polysaccharides (starch)	Disaccharides (maltose), monosaccharides
Oligosaccharidases of the intestine; brush		Small intestine	Disaccharides	Monosaccharides (e.g., glucose, fructose,

Protein

A large part of protein digestion takes place in the stomach. The enzyme pepsin plays an important role in the digestion of proteins by breaking down the intact protein to peptides, which are short chains of four to nine amino acids. In the duodenum, other enzymes—**trypsin**, **elastase**, and **chymotrypsin**—act on the peptides reducing them to smaller peptides. Trypsin elastase, carboxypeptidase, and chymotrypsin are produced by the pancreas and released into the duodenum where they act on the chyme. Further breakdown of peptides to single amino acids is aided by enzymes called peptidases (those that breakdown peptides). Specifically, **carboxypeptidase**, **dipeptidase**, and **aminopeptidase** play important roles in reducing the peptides to free amino acids. The amino acids are absorbed into the bloodstream through the small intestines. The steps in protein digestion are summarized in [\[link\]](#) and [\[link\]](#).



Digestion

of Protein

Enzyme	Produced By	Site of Action	Substrate Acting On	End Products
Pepsin	Stomach chief cells	Stomach	Proteins	Peptides
Trypsin	Pancreas	Small intestine	Proteins	Peptides
Chymotrypsin	Pancreas	Small intestine	Peptides	Amino acids and peptides
Dipeptidase	Aminopeptidase	Small intestine	Peptides	Amino acids

Lipids

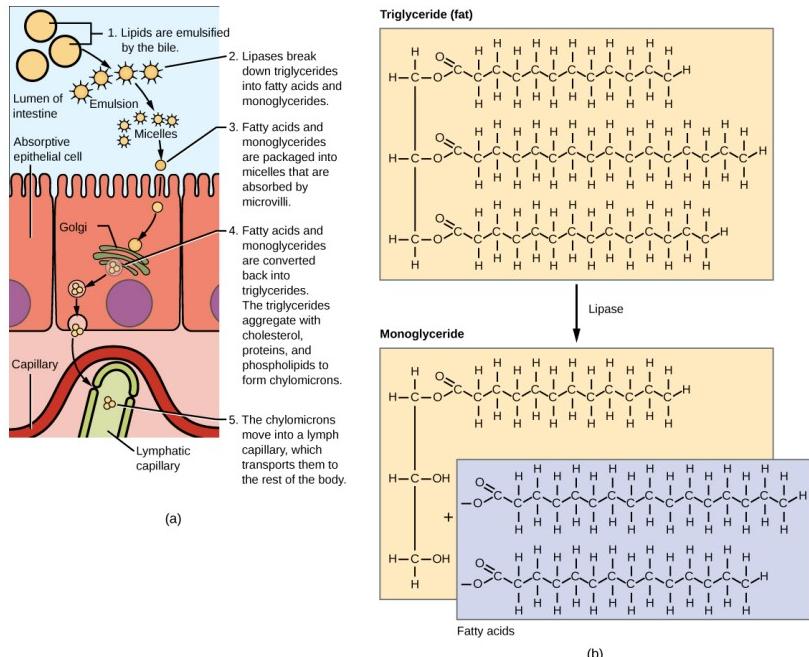
Lipid digestion begins in the stomach with the aid of lingual lipase and gastric lipase. However, the bulk of lipid digestion occurs in the small intestine due to pancreatic lipase. When chyme enters the duodenum, the hormonal responses trigger the release of bile, which is produced in the liver and stored in the gallbladder. Bile aids in the digestion of lipids, primarily triglycerides by emulsification. Emulsification is a process in which large lipid globules are broken down into several small lipid globules. These small globules are more widely distributed in the chyme rather than forming large aggregates. Lipids are hydrophobic substances: in the presence of water, they will aggregate to form

globules to minimize exposure to water. Bile contains bile salts, which are amphipathic, meaning they contain hydrophobic and hydrophilic parts. Thus, the bile salts hydrophilic side can interface with water on one side and the hydrophobic side interfaces with lipids on the other. By doing so, bile salts emulsify large lipid globules into small lipid globules.

Why is emulsification important for digestion of lipids? Pancreatic juices contain enzymes called lipases (enzymes that breakdown lipids). If the lipid in the chyme aggregates into large globules, very little surface area of the lipids is available for the lipases to act on, leaving lipid digestion incomplete. By forming an emulsion, bile salts increase the available surface area of the lipids many fold. The pancreatic lipases can then act on the lipids more efficiently and digest them, as detailed in [\[link\]](#). Lipases breakdown the lipids into fatty acids and glycerides. These molecules can pass through the plasma membrane of the cell and enter the epithelial cells of the intestinal lining. The bile salts surround long-chain fatty acids and monoglycerides forming tiny spheres called micelles. The micelles move into the brush border of the small intestine absorptive cells where the long-chain fatty acids and monoglycerides diffuse out of the micelles into the absorptive cells leaving the micelles behind in the chyme. The long-chain fatty acids and monoglycerides recombine in the absorptive cells to

form triglycerides, which aggregate into globules and become coated with proteins. These large spheres are called **chylomicrons**. Chylomicrons contain triglycerides, cholesterol, and other lipids and have proteins on their surface. The surface is also composed of the hydrophilic phosphate "heads" of phospholipids. Together, they enable the chylomicron to move in an aqueous environment without exposing the lipids to water. Chylomicrons leave the absorptive cells via exocytosis.

Chylomicrons enter the lymphatic vessels, and then enter the blood in the subclavian vein.



Vitamins

Vitamins can be either water-soluble or lipid-

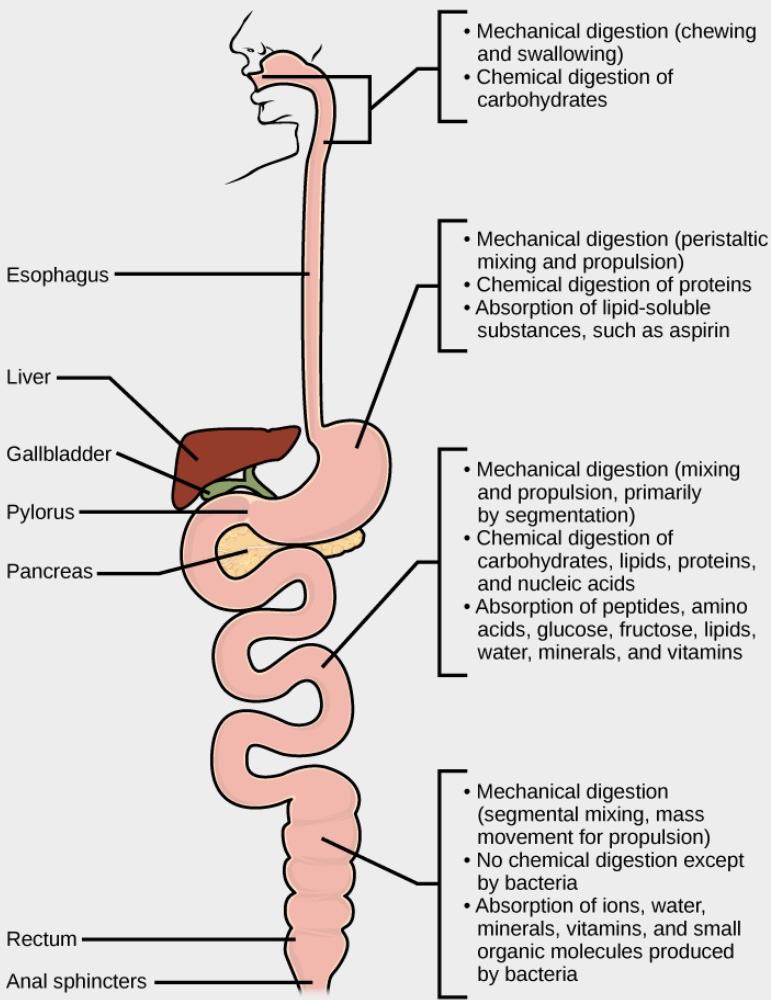
soluble. Fat soluble vitamins are absorbed in the same manner as lipids. It is important to consume some amount of dietary lipid to aid the absorption of lipid-soluble vitamins. Water-soluble vitamins can be directly absorbed into the bloodstream from the intestine.

Link to Learning

This [website](#) has an overview of the digestion of protein, fat, and carbohydrates.

Visual Connection

Mechanical and chemical digestion of food takes place in many steps, beginning in the mouth and ending in the rectum.



Which of the following statements about digestive processes is true?

1. Amylase, maltase, and lactase in the mouth digest carbohydrates.
2. Trypsin and lipase in the stomach digest protein.
3. Bile emulsifies lipids in the small intestine.
4. No food is absorbed until the small intestine.

Elimination

The final step in digestion is the elimination of undigested food content and waste products. The undigested food material enters the colon, where most of the water is reabsorbed. Recall that the colon is also home to the microflora called “intestinal flora” that aid in the digestion process. The semi-solid waste is moved through the colon by peristaltic movements of the muscle and is stored in the rectum. As the rectum expands in response to storage of fecal matter, it triggers the neural signals required to set up the urge to eliminate. The solid waste is eliminated through the anus using peristaltic movements of the rectum.

Common Problems with Elimination

Diarrhea and constipation are some of the most common health concerns that affect digestion. Constipation is a condition where the feces are hardened because of excess water removal in the colon. In contrast, if enough water is not removed from the feces, it results in diarrhea. Many bacteria, including the ones that cause cholera, affect the proteins involved in water reabsorption in the colon and result in excessive diarrhea.

Emesis

Emesis, or vomiting, is elimination of food by forceful expulsion through the mouth. It is often in response to an irritant that affects the digestive tract, including but not limited to viruses, bacteria, emotions, sights, and food poisoning. This forceful expulsion of the food is due to the strong contractions produced by the stomach muscles. The process of emesis is regulated by the medulla.

Section Summary

Digestion begins with ingestion, where the food is taken in the mouth. Digestion and absorption take place in a series of steps with special enzymes playing important roles in digesting carbohydrates, proteins, and lipids. Elimination describes removal of undigested food contents and waste products from the body. While most absorption occurs in the small intestines, the large intestine is responsible for the final removal of water that remains after the absorptive process of the small intestines. The cells that line the large intestine absorb some vitamins as well as any leftover salts and water. The large intestine (colon) is also where feces is formed.

Visual Connection Questions

[\[link\]](#) Which of the following statements about digestive processes is true?

1. Amylase, maltase, and lactase in the mouth digest carbohydrates.
 2. Trypsin and lipase in the stomach digest protein.
 3. Bile emulsifies lipids in the small intestine.
 4. No food is absorbed until the small intestine.
-

[\[link\]](#) C

Review Questions

Where does the majority of protein digestion take place?

1. stomach
 2. duodenum
 3. mouth
 4. jejunum
-

A

Lipases are enzymes that breakdown _____.

1. disaccharides
 2. lipids
 3. proteins
 4. cellulose
-

B

Which of the following conditions is most likely to cause constipation?

1. bacterial infection
 2. dehydration
 3. ulcer
 4. excessive cellulose consumption
-

B

Critical Thinking Questions

Explain why some dietary lipid is a necessary part of a balanced diet.

Lipids add flavor to food and promote a sense

of satiety or fullness. Fatty foods are sources of high energy; one gram of lipid contains nine calories. Lipids are also required in the diet to aid the absorption of lipid-soluble vitamins and for the production of lipid-soluble hormones.

The gut microbiome (the bacterial colonies in the intestines) have become a popular area of study in biomedical research. How could varying gut microbiomes impact a person's nutrition?

The gut microbiome includes all the bacteria that aid in chemical digestion in the intestines. Changing its composition can change the way that food is digested since not all bacteria have the same macromolecule-digesting enzymes. Additionally, changes in gut microbiome can lead to the establishment of pathogenic bacteria populations that cause inflammation in the gut or other disease.

Many mammals become ill if they drink milk as adults even though they could consume it as babies. What causes this digestive issue?

As mammals wean from their mothers they stop drinking milk. Since they stop consuming the

sugar lactose their bodies conserve resources by no longer making the enzyme lactase. If the animals then consume lactose at some point in the future their digestive system cannot break the lactose molecules into glucose and galactose for absorption. When gut bacteria further along the digestive tract interact with the lactose molecules it causes symptoms of lactose intolerance.

Glossary

aminopeptidase

protease that breaks down peptides to single amino acids; secreted by the brush border of small intestine

carboxypeptidase

protease that breaks down peptides to single amino acids; secreted by the brush border of the small intestine

chylomicron

small lipid globule

chymotrypsin

pancreatic protease

digestion

mechanical and chemical breakdown of food into small organic fragments

dipeptidase

protease that breaks down peptides to single amino acids; secreted by the brush border of small intestine

elastase

pancreatic protease

ingestion

act of taking in food

lactase

enzyme that breaks down lactose into glucose and galactose

maltase

enzyme that breaks down maltose into glucose

sucrase

enzyme that breaks down sucrose into glucose and fructose

trypsin

pancreatic protease that breaks down protein

Overview of the Circulatory System

By the end of this section, you will be able to:

- Describe an open and closed circulatory system
- Describe interstitial fluid and hemolymph
- Compare and contrast the organization and evolution of the vertebrate circulatory system.

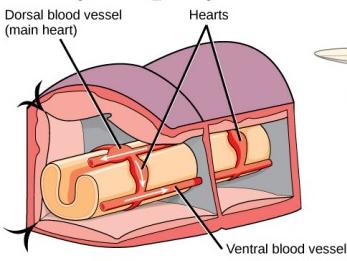
In all animals, except a few simple types, the circulatory system is used to transport nutrients and gases through the body. Simple diffusion allows some water, nutrient, waste, and gas exchange into primitive animals that are only a few cell layers thick; however, bulk flow is the only method by which the entire body of larger more complex organisms is accessed.

In (a) closed circulatory systems, the heart pumps blood through vessels that are separate from the interstitial fluid of the body. Most vertebrates and some invertebrates, like this annelid earthworm, have a closed circulatory system. In (b) open circulatory systems, a fluid called hemolymph is pumped through a blood vessel that empties into the body cavity. Hemolymph returns to the blood vessel through openings called ostia. Arthropods like this bee and most mollusks have open circulatory systems.

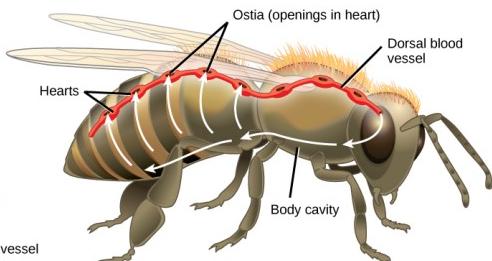
Circulatory System Architecture

The circulatory system is effectively a network of cylindrical vessels: the arteries, veins, and capillaries that emanate from a pump, the heart. In all vertebrate organisms, as well as some invertebrates, this is a closed-loop system, in which the blood is not free in a cavity. In a **closed circulatory system**, blood is contained inside blood vessels and circulates **unidirectionally** from the heart around the systemic circulatory route, then returns to the heart again, as illustrated in [\[link\]a](#). As opposed to a closed system, arthropods—including insects, crustaceans, and most mollusks—have an open circulatory system, as illustrated in [\[link\]b](#). In an **open circulatory system**, the blood is not enclosed in the blood vessels but is pumped into a cavity called a **hemocoel** and is called **hemolymph** because the blood mixes with the **interstitial fluid**. As the heart beats and the animal moves, the hemolymph circulates around the organs within the body cavity and then reenters the hearts through openings called **ostia**. This movement allows for gas and nutrient exchange. An open circulatory system does not use as much energy as a closed system to operate or to maintain; however, there is a trade-off with the amount of blood that can be moved to metabolically active organs and tissues that require high levels of oxygen. In fact, one reason that insects with wing spans of up to two feet wide (70 cm) are not around today is probably because they were outcompeted by the arrival of birds 150 million years ago. Birds, having a closed

circulatory system, are thought to have moved more agilely, allowing them to get food faster and possibly to prey on the insects.



(a) Closed circulatory system



(b) Open circulatory system

Simple animals consisting of a single cell layer such as the (a) sponge or only a few cell layers such as the (b) jellyfish do not have a circulatory system. Instead, gases, nutrients, and wastes are exchanged by diffusion. (a) Fish have the simplest circulatory systems of the vertebrates: blood flows unidirectionally from the two-chambered heart through the gills and then the rest of the body. (b) Amphibians have two circulatory routes: one for oxygenation of the blood through the lungs and skin, and the other to take oxygen to the rest of the body. The blood is pumped from a three-chambered heart with two atria and a single ventricle. (c) Reptiles also have two circulatory routes; however, blood is only oxygenated through the lungs. The heart is three chambered, but the ventricles are partially separated so some mixing of oxygenated and deoxygenated blood occurs except in crocodilians and birds. (d) Mammals and birds have the most efficient heart with four chambers that completely separate the oxygenated and deoxygenated blood; it pumps only oxygenated

blood through the body and deoxygenated blood to the lungs.

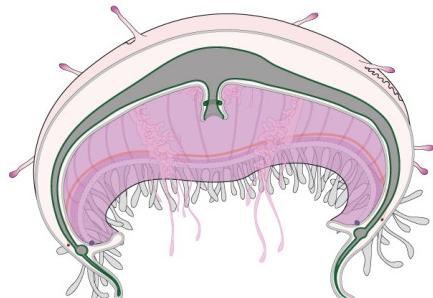
Circulatory System Variation in Animals

The circulatory system varies from simple systems in invertebrates to more complex systems in vertebrates. The simplest animals, such as the sponges (Porifera) and rotifers (Rotifera), do not need a circulatory system because diffusion allows adequate exchange of water, nutrients, and waste, as well as dissolved gases, as shown in [\[link\]a](#).

Organisms that are more complex but still only have two layers of cells in their body plan, such as jellies (Cnidaria) and comb jellies (Ctenophora) also use diffusion through their epidermis and internally through the gastrovascular compartment. Both their internal and external tissues are bathed in an aqueous environment and exchange fluids by diffusion on both sides, as illustrated in [\[link\]b](#). Exchange of fluids is assisted by the pulsing of the jellyfish body.



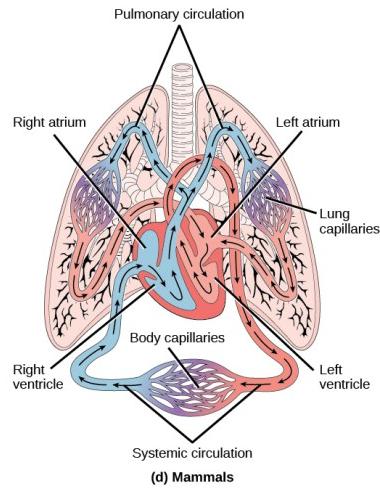
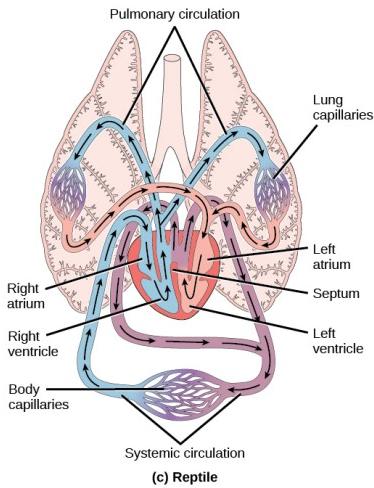
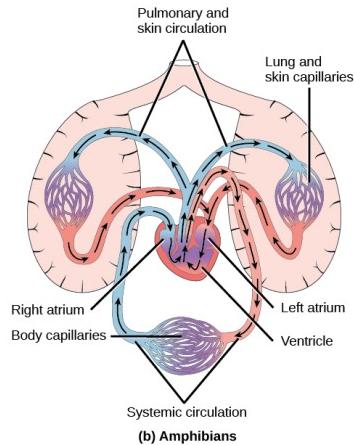
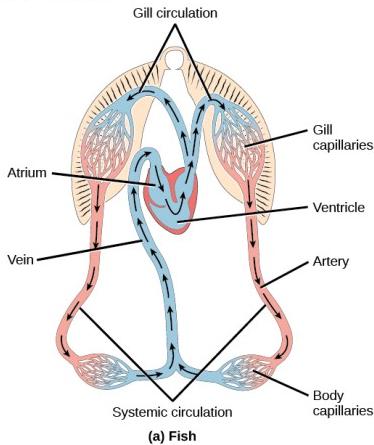
(a) Sponge



(b) Jellyfish

For more complex organisms, diffusion is not efficient for cycling gases, nutrients, and waste effectively through the body; therefore, more complex circulatory systems evolved. Most arthropods and many mollusks have open circulatory systems. In an open system, an elongated beating heart pushes the hemolymph through the body and muscle contractions help to move fluids. The larger more complex crustaceans, including lobsters, have developed arterial-like vessels to push blood through their bodies, and the most active mollusks, such as squids, have evolved a closed circulatory system and are able to move rapidly to catch prey. Closed circulatory systems are a characteristic of vertebrates; however, there are significant differences in the structure of the heart and the circulation of blood between the different vertebrate groups due to adaptation during evolution and associated differences in anatomy. [\[link\]](#) illustrates the basic circulatory systems of some vertebrates: fish, amphibians, reptiles, and

mammals.



As illustrated in [link]a Fish have a single circuit for blood flow and a two-chambered heart that has only a single atrium and a single ventricle. The atrium collects blood that has returned from the body and the ventricle pumps the blood to the gills where gas exchange occurs and the blood is re-oxygenated; this is called **gill circulation**. The blood then continues through the rest of the body before

arriving back at the atrium; this is called **systemic circulation**. This unidirectional flow of blood produces a gradient of oxygenated to deoxygenated blood around the fish's systemic circuit. The result is a limit in the amount of oxygen that can reach some of the organs and tissues of the body, reducing the overall metabolic capacity of fish.

In amphibians, reptiles, birds, and mammals, blood flow is directed in two circuits: one through the lungs and back to the heart, which is called **pulmonary circulation**, and the other throughout the rest of the body and its organs including the brain (systemic circulation). In amphibians, gas exchange also occurs through the skin during pulmonary circulation and is referred to as **pulmocutaneous circulation**.

As shown in [link]b, amphibians have a three-chambered heart that has two atria and one ventricle rather than the two-chambered heart of fish. The two **atria** (superior heart chambers) receive blood from the two different circuits (the lungs and the systems), and then there is some mixing of the blood in the heart's **ventricle** (inferior heart chamber), which reduces the efficiency of oxygenation. The advantage to this arrangement is that high pressure in the vessels pushes blood to the lungs and body. The mixing is mitigated by a ridge within the ventricle that diverts oxygen-rich blood through the systemic circulatory system and

deoxygenated blood to the pulmocutaneous circuit. For this reason, amphibians are often described as having **double circulation**.

Most reptiles also have a three-chambered heart similar to the amphibian heart that directs blood to the pulmonary and systemic circuits, as shown in [\[link\]c](#). The ventricle is divided more effectively by a partial septum, which results in less mixing of oxygenated and deoxygenated blood. Some reptiles (alligators and crocodiles) are the most primitive animals to exhibit a four-chambered heart.

Crocodilians have a unique circulatory mechanism where the heart shunts blood from the lungs toward the stomach and other organs during long periods of submergence, for instance, while the animal waits for prey or stays underwater waiting for prey to rot. One adaptation includes two main arteries that leave the same part of the heart: one takes blood to the lungs and the other provides an alternate route to the stomach and other parts of the body. Two other adaptations include a hole in the heart between the two ventricles, called the foramen of Panizza, which allows blood to move from one side of the heart to the other, and specialized connective tissue that slows the blood flow to the lungs. Together these adaptations have made crocodiles and alligators one of the most evolutionarily successful animal groups on earth.

In mammals and birds, the heart is also divided into

four chambers: two atria and two ventricles, as illustrated in [link]d. The oxygenated blood is separated from the deoxygenated blood, which improves the efficiency of double circulation and is probably required for the warm-blooded lifestyle of mammals and birds. The four-chambered heart of birds and mammals evolved independently from a three-chambered heart. The independent evolution of the same or a similar biological trait is referred to as convergent evolution.

Section Summary

In most animals, the circulatory system is used to transport blood through the body. Some primitive animals use diffusion for the exchange of water, nutrients, and gases. However, complex organisms use the circulatory system to carry gases, nutrients, and waste through the body. Circulatory systems may be open (mixed with the interstitial fluid) or closed (separated from the interstitial fluid). Closed circulatory systems are a characteristic of vertebrates; however, there are significant differences in the structure of the heart and the circulation of blood between the different vertebrate groups due to adaptions during evolution and associated differences in anatomy. Fish have a two-chambered heart with unidirectional circulation. Amphibians have a three-chambered heart, which has some mixing of the blood, and they have double

circulation. Most non-avian reptiles have a three-chambered heart, but have little mixing of the blood; they have double circulation. Mammals and birds have a four-chambered heart with no mixing of the blood and double circulation.

Review Questions

Why are open circulatory systems advantageous to some animals?

1. They use less metabolic energy.
 2. They help the animal move faster.
 3. They do not need a heart.
 4. They help large insects develop.
-

A

Some animals use diffusion instead of a circulatory system. Examples include:

1. birds and jellyfish
 2. flatworms and arthropods
 3. mollusks and jellyfish
 4. None of the above
-

D

Blood flow that is directed through the lungs and back to the heart is called ____.

1. unidirectional circulation
 2. gill circulation
 3. pulmonary circulation
 4. pulmocutaneous circulation
-

C

Free Response

Describe a closed circulatory system.

A closed circulatory system is a closed-loop system, in which blood is not free in a cavity. Blood is separate from the bodily interstitial fluid and contained within blood vessels. In this type of system, blood circulates unidirectionally from the heart around the systemic circulatory route, and then returns to the heart.

Describe systemic circulation.

Systemic circulation flows through the systems of the body. The blood flows away from the heart to the brain, liver, kidneys, stomach, and other organs, the limbs, and the muscles of the body; it then returns to the heart.

Glossary

atrium

(plural: atria) chamber of the heart that receives blood from the veins and sends blood to the ventricles

closed circulatory system

system in which the blood is separated from the bodily interstitial fluid and contained in blood vessels

double circulation

flow of blood in two circuits: the pulmonary circuit through the lungs and the systemic circuit through the organs and body

gill circulation

circulatory system that is specific to animals with gills for gas exchange; the blood flows through the gills for oxygenation

hemocoel

cavity into which blood is pumped in an open

circulatory system

hemolymph

mixture of blood and interstitial fluid that is found in insects and other arthropods as well as most mollusks

interstitial fluid

fluid between cells

open circulatory system

system in which the blood is mixed with interstitial fluid and directly covers the organs

ostium

(plural: ostia) holes between blood vessels that allow the movement of hemolymph through the body of insects, arthropods, and mollusks with open circulatory systems

pulmocutaneous circulation

circulatory system in amphibians; the flow of blood to the lungs and the moist skin for gas exchange

pulmonary circulation

flow of blood away from the heart through the lungs where oxygenation occurs and then returns to the heart again

systemic circulation

flow of blood away from the heart to the brain, liver, kidneys, stomach, and other organs, the limbs, and the muscles of the body, and then the return of this blood to the heart

unidirectional circulation

flow of blood in a single circuit; occurs in fish where the blood flows through the gills, then past the organs and the rest of the body, before returning to the heart

ventricle

(heart) large inferior chamber of the heart that pumps blood into arteries

Components of the Blood

By the end of this section, you will be able to:

- List the basic components of the blood
- Compare red and white blood cells
- Describe blood plasma and serum

Hemoglobin is responsible for distributing oxygen, and to a lesser extent, carbon dioxide, throughout the circulatory systems of humans, vertebrates, and many invertebrates. The blood is more than the proteins, though. Blood is actually a term used to describe the liquid that moves through the vessels and includes **plasma** (the liquid portion, which contains water, proteins, salts, lipids, and glucose) and the cells (red and white cells) and cell fragments called **platelets**. Blood plasma is actually the dominant component of blood and contains the water, proteins, electrolytes, lipids, and glucose. The cells are responsible for carrying the gases (red cells) and immune the response (white). The platelets are responsible for blood clotting.

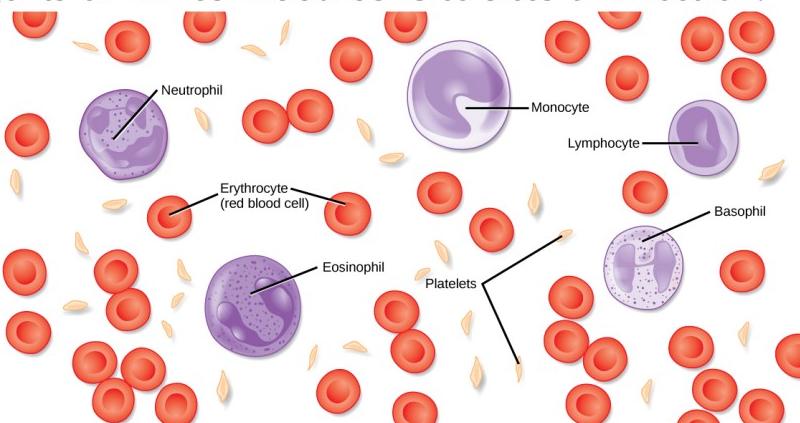
Interstitial fluid that surrounds cells is separate from the blood, but in hemolymph, they are combined. In humans, cellular components make up approximately 45 percent of the blood and the liquid plasma 55 percent. Blood is 20 percent of a person's extracellular fluid and eight percent of weight.

The cells and cellular components of human blood are shown. Red blood cells deliver oxygen to the

cells and remove carbon dioxide. White blood cells—including neutrophils, monocytes, lymphocytes, eosinophils, and basophils—are involved in the immune response. Platelets form clots that prevent blood loss after injury.

The Role of Blood in the Body

Blood, like the human blood illustrated in [link] is important for regulation of the body's systems and homeostasis. Blood helps maintain homeostasis by stabilizing pH, temperature, osmotic pressure, and by eliminating excess heat. Blood supports growth by distributing nutrients and hormones, and by removing waste. Blood plays a protective role by transporting clotting factors and platelets to prevent blood loss and transporting the disease-fighting agents or **white blood cells** to sites of infection.



In most vertebrates, (a) hemoglobin delivers oxygen to the body and removes some carbon dioxide. Hemoglobin is composed of four protein subunits,

two alpha chains and two beta chains, and a heme group that has iron associated with it. The iron reversibly associates with oxygen, and in so doing is oxidized from Fe^{2+} to Fe^{3+} . In most mollusks and some arthropods, (b) hemocyanin delivers oxygen. Unlike hemoglobin, hemolymph is not carried in blood cells, but floats free in the hemolymph. Copper instead of iron binds the oxygen, giving the hemolymph a blue-green color. In annelids, such as the earthworm, and some other invertebrates, (c) hemerythrin carries oxygen. Like hemoglobin, hemerythrin is carried in blood cells and has iron associated with it, but despite its name, hemerythrin does not contain heme.

Red Blood Cells

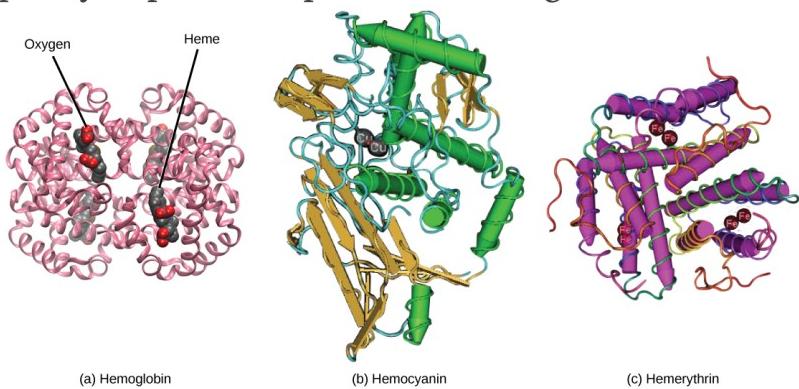
Red blood cells, or erythrocytes (*erythro-* = “red”; *-cyte* = “cell”), are specialized cells that circulate through the body delivering oxygen to cells; they are formed from stem cells in the bone marrow. In mammals, red blood cells are small biconcave cells that at maturity do not contain a nucleus or mitochondria and are only 7–8 μm in size. In birds and non-avian reptiles, a nucleus is still maintained in red blood cells.

The red coloring of blood comes from the iron-containing protein hemoglobin, illustrated in [\[link\]a](#). The principal job of this protein is to carry oxygen, but it also transports carbon dioxide as

well. Hemoglobin is packed into red blood cells at a rate of about 250 million molecules of hemoglobin per cell. Each hemoglobin molecule binds four oxygen molecules so that each red blood cell carries one billion molecules of oxygen. There are approximately 25 trillion red blood cells in the five liters of blood in the human body, which could carry up to 25 sextillion (25×10^{21}) molecules of oxygen in the body at any time. In mammals, the lack of organelles in erythrocytes leaves more room for the hemoglobin molecules, and the lack of mitochondria also prevents use of the oxygen for metabolic respiration. Only mammals have anucleated red blood cells, and some mammals (camels, for instance) even have nucleated red blood cells. The advantage of nucleated red blood cells is that these cells can undergo mitosis. Anucleated red blood cells metabolize anaerobically (without oxygen), making use of a primitive metabolic pathway to produce ATP and increase the efficiency of oxygen transport.

Not all organisms use hemoglobin as the method of oxygen transport. Invertebrates that utilize hemolymph rather than blood use different pigments to bind to the oxygen. These pigments use copper or iron to the oxygen. Invertebrates have a variety of other respiratory pigments. Hemocyanin, a blue-green, copper-containing protein, illustrated in [link]b is found in mollusks, crustaceans, and some of the arthropods. Chlorocruorin, a green-

colored, iron-containing pigment is found in four families of polychaete tubeworms. Hemerythrin, a red, iron-containing protein is found in some polychaete worms and annelids and is illustrated in [link]c. Despite the name, hemerythrin does not contain a heme group and its oxygen-carrying capacity is poor compared to hemoglobin.



The small size and large surface area of red blood cells allows for rapid diffusion of oxygen and carbon dioxide across the plasma membrane. In the lungs, carbon dioxide is released and oxygen is taken in by the blood. In the tissues, oxygen is released from the blood and carbon dioxide is bound for transport back to the lungs. Studies have found that hemoglobin also binds nitrous oxide (NO). NO is a vasodilator that relaxes the blood vessels and capillaries and may help with gas exchange and the passage of red blood cells through narrow vessels. Nitroglycerin, a heart medication for angina and heart attacks, is converted to NO to help relax the blood vessels and increase oxygen flow through the body.

A characteristic of red blood cells is their glycolipid and glycoprotein coating; these are lipids and proteins that have carbohydrate molecules attached. In humans, the surface glycoproteins and glycolipids on red blood cells vary between individuals, producing the different blood types, such as A, B, and O. Red blood cells have an average life span of 120 days, at which time they are broken down and recycled in the liver and spleen by phagocytic macrophages, a type of white blood cell.

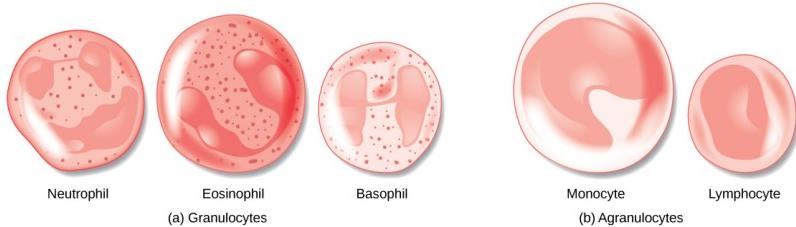
(a) Granulocytes—including neutrophils, eosinophils and basophils—are characterized by a lobed nucleus and granular inclusions in the cytoplasm. Granulocytes are typically first-responders during injury or infection. (b) Agranulocytes include lymphocytes and monocytes. Lymphocytes, including B and T cells, are responsible for adaptive immune response. Monocytes differentiate into macrophages and dendritic cells, which in turn respond to infection or injury.

White Blood Cells

White blood cells, also called leukocytes (leuko = white), make up approximately one percent by volume of the cells in blood. The role of white blood cells is very different than that of red blood cells: they are primarily involved in the immune response to identify and target pathogens, such as invading bacteria, viruses, and other foreign organisms.

White blood cells are formed continually; some only live for hours or days, but some live for years.

The morphology of white blood cells differs significantly from red blood cells. They have nuclei and do not contain hemoglobin. The different types of white blood cells are identified by their microscopic appearance after histologic staining, and each has a different specialized function. The two main groups, both illustrated in [\[link\]](#) are the granulocytes, which include the neutrophils, eosinophils, and basophils, and the agranulocytes, which include the monocytes and lymphocytes.



Granulocytes contain granules in their cytoplasm; the agranulocytes are so named because of the lack of granules in their cytoplasm. Some leukocytes become macrophages that either stay at the same site or move through the blood stream and gather at sites of infection or inflammation where they are attracted by chemical signals from foreign particles and damaged cells. Lymphocytes are the primary cells of the immune system and include B cells, T cells, and natural killer cells. B cells destroy bacteria and inactivate their toxins. They also produce antibodies. T cells attack viruses, fungi, some

bacteria, transplanted cells, and cancer cells. T cells attack viruses by releasing toxins that kill the viruses. Natural killer cells attack a variety of infectious microbes and certain tumor cells.

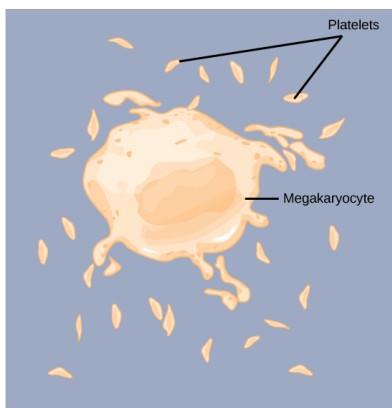
One reason that HIV poses significant management challenges is because the virus directly targets T cells by gaining entry through a receptor. Once inside the cell, HIV then multiplies using the T cell's own genetic machinery. After the HIV virus replicates, it is transmitted directly from the infected T cell to macrophages. The presence of HIV can remain unrecognized for an extensive period of time before full disease symptoms develop.

(a) Platelets are formed from large cells called megakaryocytes. The megakaryocyte breaks up into thousands of fragments that become platelets. (b) Platelets are required for clotting of the blood. The platelets collect at a wound site in conjunction with other clotting factors, such as fibrinogen, to form a fibrin clot that prevents blood loss and allows the wound to heal.

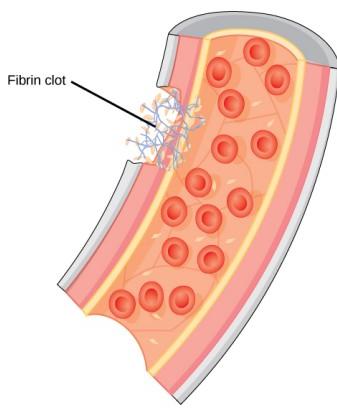
Platelets and Coagulation Factors

Blood must clot to heal wounds and prevent excess blood loss. Small cell fragments called platelets (thrombocytes) are attracted to the wound site where they adhere by extending many projections and releasing their contents. These contents activate other platelets and also interact with other

coagulation factors, which convert fibrinogen, a water-soluble protein present in blood serum into fibrin (a non-water soluble protein), causing the blood to clot. Many of the clotting factors require vitamin K to work, and vitamin K deficiency can lead to problems with blood clotting. Many platelets converge and stick together at the wound site forming a platelet plug (also called a fibrin clot), as illustrated in [link]b. The plug or clot lasts for a number of days and stops the loss of blood. Platelets are formed from the disintegration of larger cells called megakaryocytes, like that shown in [link]a. For each megakaryocyte, 2000–3000 platelets are formed with 150,000 to 400,000 platelets present in each cubic millimeter of blood. Each platelet is disc shaped and 2–4 μm in diameter. They contain many small vesicles but do not contain a nucleus.



(a)



(b)

Plasma and Serum

The liquid component of blood is called plasma, and it is separated by spinning or centrifuging the blood at high rotations (3000 rpm or higher). The blood cells and platelets are separated by centrifugal forces to the bottom of a specimen tube. The upper liquid layer, the plasma, consists of 90 percent water along with various substances required for maintaining the body's pH, osmotic load, and for protecting the body. The plasma also contains the coagulation factors and antibodies.

The plasma component of blood without the coagulation factors is called the **serum**. Serum is similar to interstitial fluid in which the correct composition of key ions acting as electrolytes is essential for normal functioning of muscles and nerves. Other components in the serum include proteins that assist with maintaining pH and osmotic balance while giving viscosity to the blood. The serum also contains antibodies, specialized proteins that are important for defense against viruses and bacteria. Lipids, including cholesterol, are also transported in the serum, along with various other substances including nutrients, hormones, metabolic waste, plus external substances, such as, drugs, viruses, and bacteria.

Human serum albumin is the most abundant protein in human blood plasma and is synthesized in the liver. Albumin, which constitutes about half of the blood serum protein, transports hormones and fatty

acids, buffers pH, and maintains osmotic pressures. Immunoglobulin is a protein antibody produced in the mucosal lining and plays an important role in antibody mediated immunity.

Evolution Connection

Blood Types Related to Proteins on the Surface of the Red Blood Cells

Red blood cells are coated in antigens made of glycolipids and glycoproteins. The composition of these molecules is determined by genetics, which have evolved over time. In humans, the different surface antigens are grouped into 24 different blood groups with more than 100 different antigens on each red blood cell. The two most well known blood groups are the ABO, shown in [\[link\]](#), and Rh systems. The surface antigens in the ABO blood group are glycolipids, called antigen A and antigen B. People with blood type A have antigen A, those with blood type B have antigen B, those with blood type AB have both antigens, and people with blood type O have neither antigen. Antibodies called agglutinogens are found in the blood plasma and react with the A or B antigens, if the two are mixed. When type A and type B blood are combined, agglutination (clumping) of the blood occurs because of antibodies in the plasma that bind with the opposing antigen; this causes clots that coagulate in the kidney causing kidney failure.

Type O blood has neither A or B antigens, and therefore, type O blood can be given to all blood types. Type O negative blood is the universal donor. Type AB positive blood is the universal acceptor because it has both A and B antigen. The ABO blood groups were discovered in 1900 and 1901 by Karl Landsteiner at the University of Vienna.

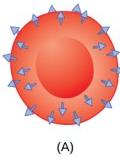
The Rh blood group was first discovered in Rhesus monkeys. Most people have the Rh antigen (Rh +) and do not have anti-Rh antibodies in their blood. The few people who do not have the Rh antigen and are Rh- can develop anti-Rh antibodies if exposed to Rh + blood. This can happen after a blood transfusion or after an Rh- woman has an Rh + baby. The first exposure does not usually cause a reaction; however, at the second exposure, enough antibodies have built up in the blood to produce a reaction that causes agglutination and breakdown of red blood cells. An injection can prevent this reaction.

Human red blood cells may have either type A or B glycoproteins on their surface, both glycoproteins combined (AB), or neither (O). The glycoproteins serve as antigens and can elicit an immune response in a person who receives a transfusion containing unfamiliar antigens. Type O blood, which has no A or B antigens, does not elicit an immune response when injected into a person of any blood type. Thus, O is considered the universal donor. Persons with type AB blood can accept

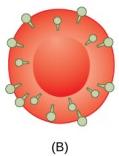
blood from any blood type, and type AB is considered the universal acceptor.



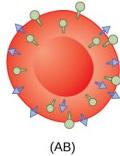
(O)



(A)



(B)



(AB)

Link to Learning



Play a blood typing game on the [Nobel Prize website](#) to solidify your understanding of blood types.

Section Summary

Specific components of the blood include red blood cells, white blood cells, platelets, and the plasma, which contains coagulation factors and serum.

Blood is important for regulation of the body's pH, temperature, osmotic pressure, the circulation of nutrients and removal of waste, the distribution of hormones from endocrine glands, and the elimination of excess heat; it also contains components for blood clotting. Red blood cells are specialized cells that contain hemoglobin and circulate through the body delivering oxygen to cells. White blood cells are involved in the immune response to identify and target invading bacteria, viruses, and other foreign organisms; they also recycle waste components, such as old red blood cells. Platelets and blood clotting factors cause the change of the soluble protein fibrinogen to the insoluble protein fibrin at a wound site forming a plug. Plasma consists of 90 percent water along with various substances, such as coagulation factors and antibodies. The serum is the plasma component of the blood without the coagulation factors.

Review Questions

White blood cells:

1. can be classified as granulocytes or agranulocytes
2. defend the body against bacteria and viruses

-
- 3. are also called leucocytes
 - 4. All of the above

D

Platelet plug formation occurs at which point?

- 1. when large megakaryocytes break up into thousands of smaller fragments
 - 2. when platelets are dispersed through the blood stream
 - 3. when platelets are attracted to a site of blood vessel damage
 - 4. none of the above
-

C

In humans, the plasma comprises what percentage of the blood?

- 1. 45 percent
 - 2. 55 percent
 - 3. 25 percent
 - 4. 90 percent
-

B

The red blood cells of birds differ from mammalian red blood cells because:

1. they are white and have nuclei
 2. they do not have nuclei
 3. they have nuclei
 4. they fight disease
-

C

Free Response

Describe the cause of different blood type groups.

Red blood cells are coated with proteins called antigens made of glycolipids and glycoproteins. When type A and type B blood are mixed, the blood agglutinates because of antibodies in the plasma that bind with the opposing antigen. Type O blood has no antigens. The Rh blood group has either the Rh antigen (Rh+) or no Rh antigen (Rh-).

List some of the functions of blood in the body.

Blood is important for regulation of the body's pH, temperature, and osmotic pressure, the circulation of nutrients and removal of wastes, the distribution of hormones from endocrine glands, the elimination of excess heat; it also contains components for the clotting of blood to prevent blood loss. Blood also transports clotting factors and disease-fighting agents.

How does the lymphatic system work with blood flow?

Lymph capillaries take fluid from the blood to the lymph nodes. The lymph nodes filter the lymph by percolation through connective tissue filled with white blood cells. The white blood cells remove infectious agents, such as bacteria and viruses, to clean the lymph before it returns to the bloodstream.

Glossary

plasma

liquid component of blood that is left after the cells are removed

platelet

(also, thrombocyte) small cellular fragment

that collects at wounds, cross-reacts with clotting factors, and forms a plug to prevent blood loss

red blood cell

small (7–8 μm) biconcave cell without mitochondria (and in mammals without nuclei) that is packed with hemoglobin, giving the cell its red color; transports oxygen through the body

serum

plasma without the coagulation factors

white blood cell

large (30 μm) cell with nuclei of which there are many types with different roles including the protection of the body from viruses and bacteria, and cleaning up dead cells and other waste

Mammalian Heart and Blood Vessels

By the end of this section, you will be able to:

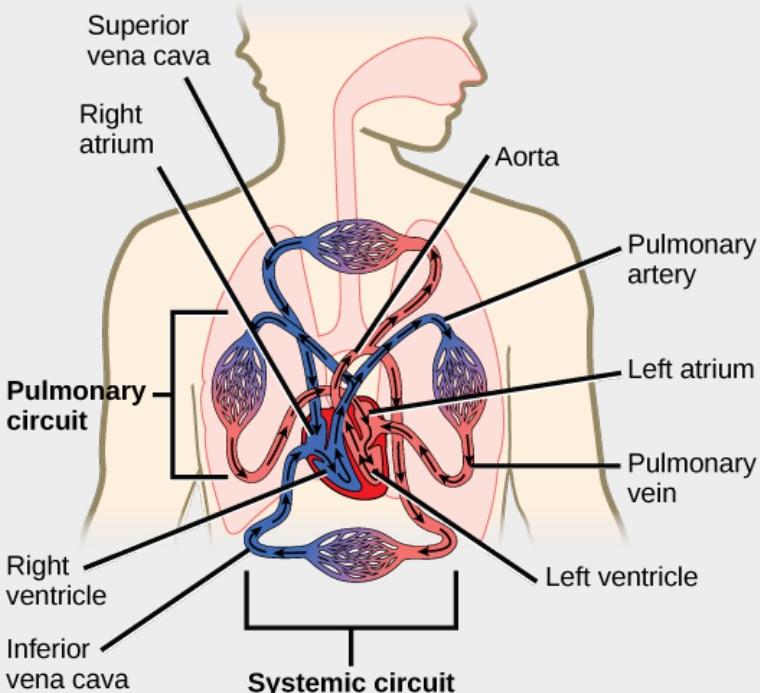
- Describe the structure of the heart and explain how cardiac muscle is different from other muscles
- Describe the cardiac cycle
- Explain the structure of arteries, veins, and capillaries, and how blood flows through the body

The heart is a complex muscle that pumps blood through the three divisions of the circulatory system: the coronary (vessels that serve the heart), pulmonary (heart and lungs), and systemic (systems of the body), as shown in [\[link\]](#). Coronary circulation intrinsic to the heart takes blood directly from the main artery (aorta) coming from the heart. For pulmonary and systemic circulation, the heart has to pump blood to the lungs or the rest of the body, respectively. In vertebrates, the lungs are relatively close to the heart in the thoracic cavity. The shorter distance to pump means that the muscle wall on the right side of the heart is not as thick as the left side which must have enough pressure to pump blood all the way to your big toe.

Art Connection

The mammalian circulatory system is divided into

three circuits: the systemic circuit, the pulmonary circuit, and the coronary circuit. Blood is pumped from veins of the systemic circuit into the right atrium of the heart, then into the right ventricle. Blood then enters the pulmonary circuit, and is oxygenated by the lungs. From the pulmonary circuit, blood re-enters the heart through the left atrium. From the left ventricle, blood re-enters the systemic circuit through the aorta and is distributed to the rest of the body. The coronary circuit, which provides blood to the heart, is not shown.



Which of the following statements about the circulatory system is false?

1. Blood in the pulmonary vein is deoxygenated.

2. Blood in the inferior vena cava is deoxygenated.
3. Blood in the pulmonary artery is deoxygenated.
4. Blood in the aorta is oxygenated.

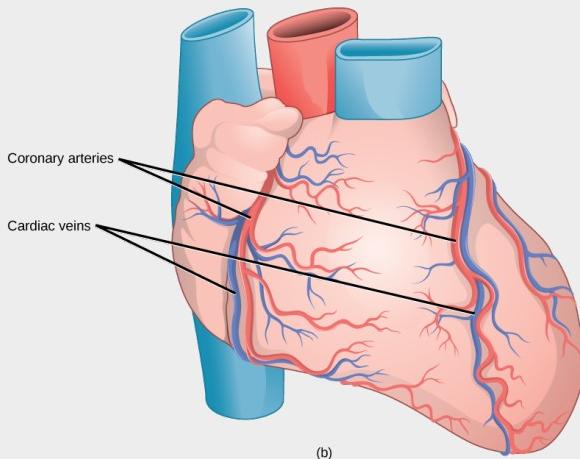
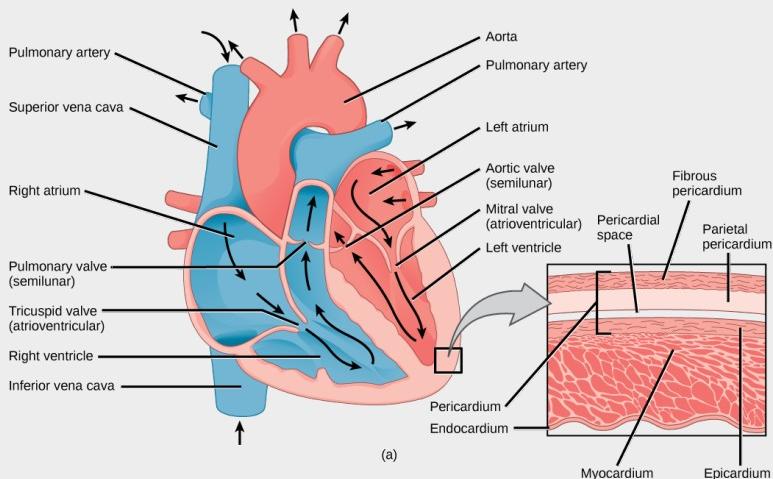
Structure of the Heart

The heart muscle is asymmetrical as a result of the distance blood must travel in the pulmonary and systemic circuits. Since the right side of the heart sends blood to the pulmonary circuit it is smaller than the left side which must send blood out to the whole body in the systemic circuit, as shown in [\[link\]](#). In humans, the heart is about the size of a clenched fist; it is divided into four chambers: two atria and two ventricles. There is one atrium and one ventricle on the right side and one atrium and one ventricle on the left side. The atria are the chambers that receive blood, and the ventricles are the chambers that pump blood. The right atrium receives deoxygenated blood from the **superior vena cava**, which drains blood from the jugular vein that comes from the brain and from the veins that come from the arms, as well as from the **inferior vena cava** which drains blood from the veins that come from the lower organs and the legs.

In addition, the right atrium receives blood from the coronary sinus which drains deoxygenated blood from the heart itself. This deoxygenated blood then passes to the right ventricle through the **atrioventricular valve** or the **tricuspid valve**, a flap of connective tissue that opens in only one direction to prevent the backflow of blood. The valve separating the chambers on the left side of the heart valve is called the biscuspid or mitral valve. After it is filled, the right ventricle pumps the blood through the pulmonary arteries, by-passing the **semilunar valve** (or pulmonic valve) to the lungs for re-oxygenation. After blood passes through the pulmonary arteries, the right semilunar valves close preventing the blood from flowing backwards into the right ventricle. The left atrium then receives the oxygen-rich blood from the lungs via the pulmonary veins. This blood passes through the **bicuspid valve** or mitral valve (the atrioventricular valve on the left side of the heart) to the left ventricle where the blood is pumped out through **aorta**, the major artery of the body, taking oxygenated blood to the organs and muscles of the body. Once blood is pumped out of the left ventricle and into the aorta, the aortic semilunar valve (or aortic valve) closes preventing blood from flowing backward into the left ventricle. This pattern of pumping is referred to as double circulation and is found in all mammals.

Art Connection

(a) The heart is primarily made of a thick muscle layer, called the myocardium, surrounded by membranes. One-way valves separate the four chambers. (b) Blood vessels of the coronary system, including the coronary arteries and veins, keep the heart musculature oxygenated.



Which of the following statements about the heart is false?

1. The mitral valve separates the left ventricle from the left atrium.
2. Blood travels through the bicuspid valve to the left atrium.
3. Both the aortic and the pulmonary valves are semilunar valves.
4. The mitral valve is an atrioventricular valve.

The heart is composed of three layers; the epicardium, the myocardium, and the endocardium, illustrated in [\[link\]](#). The inner wall of the heart has a lining called the **endocardium**. The **myocardium** consists of the heart muscle cells that make up the middle layer and the bulk of the heart wall. The outer layer of cells is called the **epicardium**, of which the second layer is a membranous layered structure called the **pericardium** that surrounds and protects the heart; it allows enough room for vigorous pumping but also keeps the heart in place to reduce friction between the heart and other structures.

The heart has its own blood vessels that supply the heart muscle with blood. The **coronary arteries** branch from the aorta and surround the outer surface of the heart like a crown. They diverge into capillaries where the heart muscle is supplied with oxygen before converging again into the **coronary veins** to take the deoxygenated blood back to the

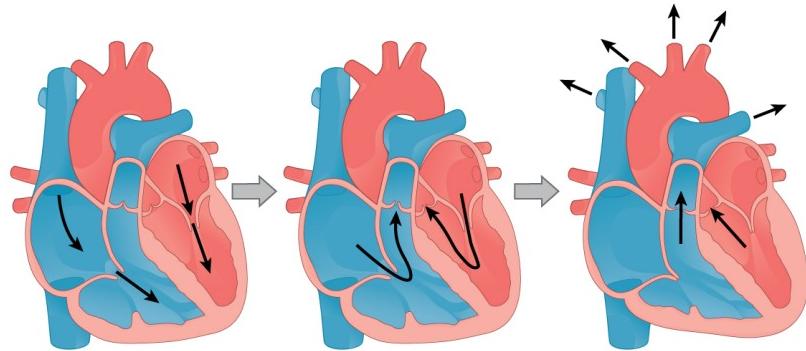
right atrium where the blood will be re-oxygenated through the pulmonary circuit. The heart muscle will die without a steady supply of blood.

Atherosclerosis is the blockage of an artery by the buildup of fatty plaques. Because of the size (narrow) of the coronary arteries and their function in serving the heart itself, atherosclerosis can be deadly in these arteries. The slowdown of blood flow and subsequent oxygen deprivation that results from atherosclerosis causes severe pain, known as **angina**, and complete blockage of the arteries will cause **myocardial infarction**: the death of cardiac muscle tissue, commonly known as a heart attack.

During (a) cardiac diastole, the heart muscle is relaxed and blood flows into the heart. During (b) atrial systole, the atria contract, pushing blood into the ventricles. During (c) atrial diastole, the ventricles contract, forcing blood out of the heart. Cardiomyocytes are striated muscle cells found in cardiac tissue. (credit: modification of work by Dr. S. Girod, Anton Becker; scale-bar data from Matt Russell) The beating of the heart is regulated by an electrical impulse that causes the characteristic reading of an ECG. The signal is initiated at the sinoatrial valve. The signal then (a) spreads to the atria, causing them to contract. The signal is (b) delayed at the atrioventricular node before it is passed on to the (c) heart apex. The delay allows the atria to relax before the (d) ventricles contract. The final part of the ECG cycle prepares the heart for the next beat.

The Cardiac Cycle

The main purpose of the heart is to pump blood through the body; it does so in a repeating sequence called the cardiac cycle. The **cardiac cycle** is the coordination of the filling and emptying of the heart of blood by electrical signals that cause the heart muscles to contract and relax. The human heart beats over 100,000 times per day. In each cardiac cycle, the heart contracts (**systole**), pushing out the blood and pumping it through the body; this is followed by a relaxation phase (**diastole**), where the heart fills with blood, as illustrated in [\[link\]](#). The atria contract at the same time, forcing blood through the atrioventricular valves into the ventricles. Closing of the atrioventricular valves produces a monosyllabic “lup” sound. Following a brief delay, the ventricles contract at the same time forcing blood through the semilunar valves into the aorta and the artery transporting blood to the lungs (via the pulmonary artery). Closing of the semilunar valves produces a monosyllabic “dup” sound.

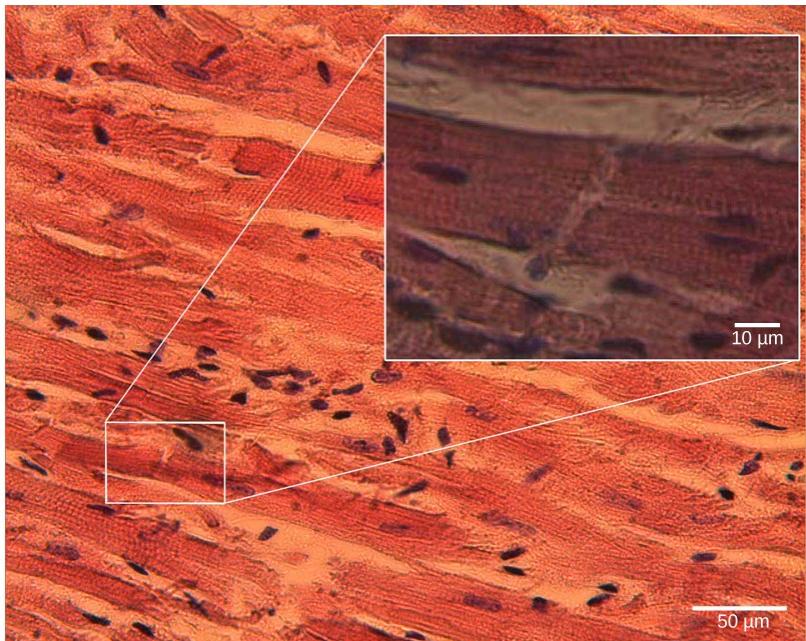


(a) **Cardiac diastole:** all chambers are relaxed, and blood flows into the heart.

(b) **Atrial systole, ventricular diastole:** atria contract, pushing blood into the ventricles.

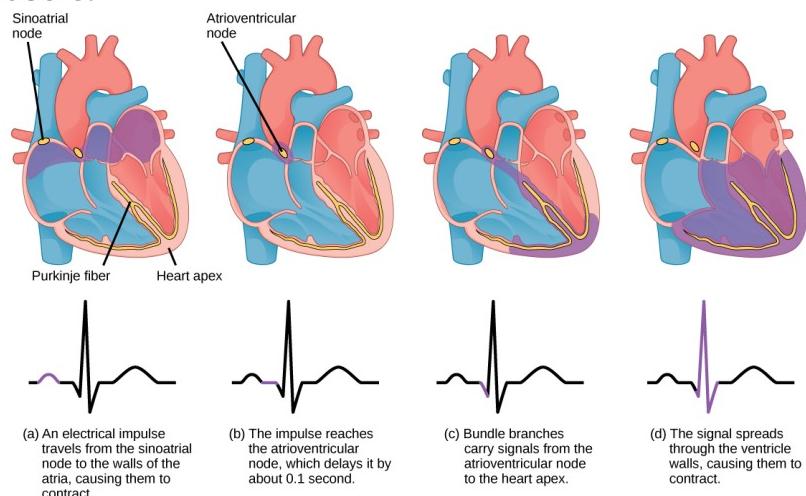
(c) **Atrial diastole, ventricular systole:** after the atria relax, the ventricles contract, pushing blood out of the heart.

The pumping of the heart is a function of the cardiac muscle cells, or cardiomyocytes, that make up the heart muscle. **Cardiomyocytes**, shown in [\[link\]](#), are distinctive muscle cells that are striated like skeletal muscle but pump rhythmically and involuntarily like smooth muscle; they are connected by intercalated disks exclusive to cardiac muscle. They are self-stimulated for a period of time and isolated cardiomyocytes will beat if given the correct balance of nutrients and electrolytes.



The autonomous beating of cardiac muscle cells is regulated by the heart's internal pacemaker that uses electrical signals to time the beating of the heart. The electrical signals and mechanical actions, illustrated in [\[link\]](#), are intimately intertwined. The internal pacemaker starts at the **sinoatrial (SA) node**, which is located near the wall of the right atrium. Electrical charges spontaneously pulse from the SA node causing the two atria to contract in unison. The pulse reaches a second node, called the atrioventricular (AV) node, between the right atrium and right ventricle where it pauses for approximately 0.1 second before spreading to the walls of the ventricles. From the AV node, the electrical impulse enters the bundle of His, then to the left and right bundle branches extending

through the interventricular septum. Finally, the Purkinje fibers conduct the impulse from the apex of the heart up the ventricular myocardium, and then the ventricles contract. This pause allows the atria to empty completely into the ventricles before the ventricles pump out the blood. The electrical impulses in the heart produce electrical currents that flow through the body and can be measured on the skin using electrodes. This information can be observed as an **electrocardiogram (ECG)**—a recording of the electrical impulses of the cardiac muscle.



Link to Learning



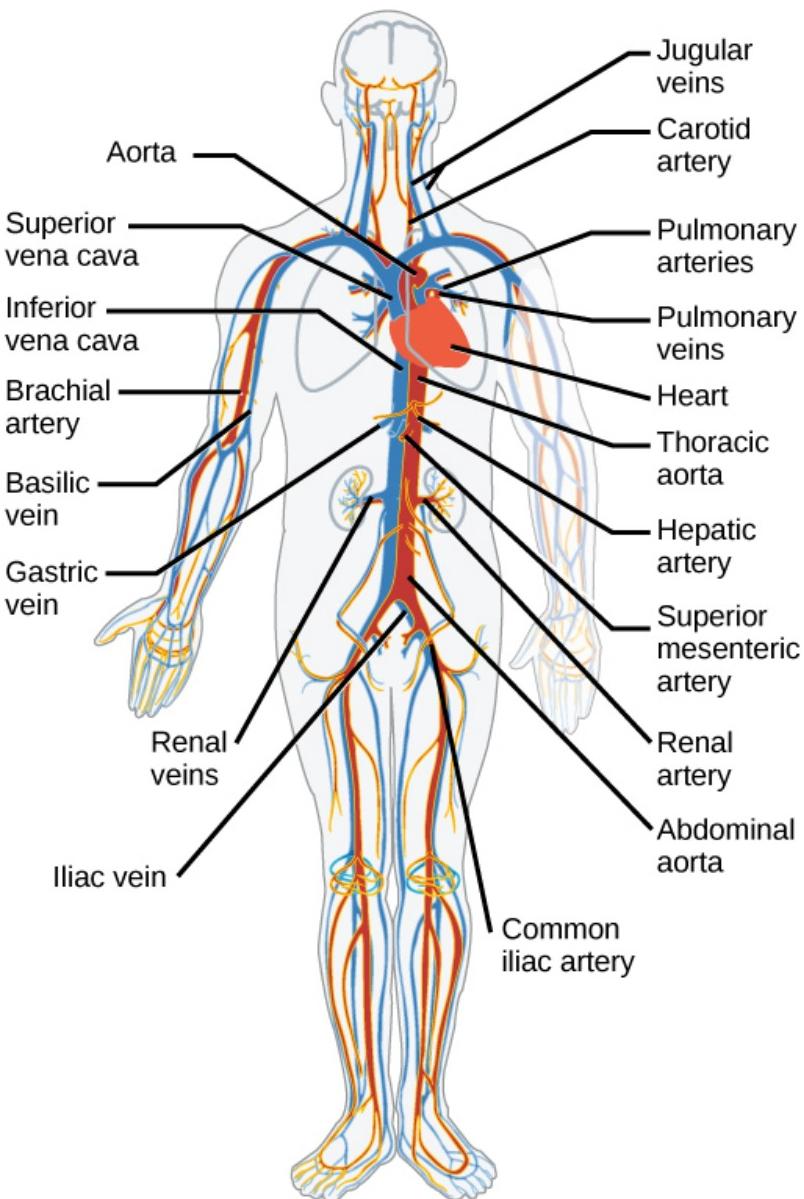
Visit [this site](#) and select the dropdown “Your Heart’s Electrical System” to see the heart’s “pacemaker” in action.

The major human arteries and veins are shown. (credit: modification of work by Mariana Ruiz Villareal) Arteries and veins consist of three layers: an outer tunica externa, a middle tunica media, and an inner tunica intima. Capillaries consist of a single layer of epithelial cells, the tunica intima. (credit: modification of work by NCI, NIH)

Arteries, Veins, and Capillaries

The blood from the heart is carried through the body by a complex network of blood vessels ([\[link\]](#)). **Arteries** take blood away from the heart. The main artery is the aorta that branches into major arteries that take blood to different limbs and organs. These major arteries include the carotid artery that takes blood to the brain, the brachial arteries that take blood to the arms, and the thoracic artery that takes blood to the thorax and

then into the hepatic, renal, and gastric arteries for the liver, kidney, and stomach, respectively. The iliac artery takes blood to the lower limbs. The major arteries diverge into minor arteries, and then smaller vessels called **arterioles**, to reach more deeply into the muscles and organs of the body.

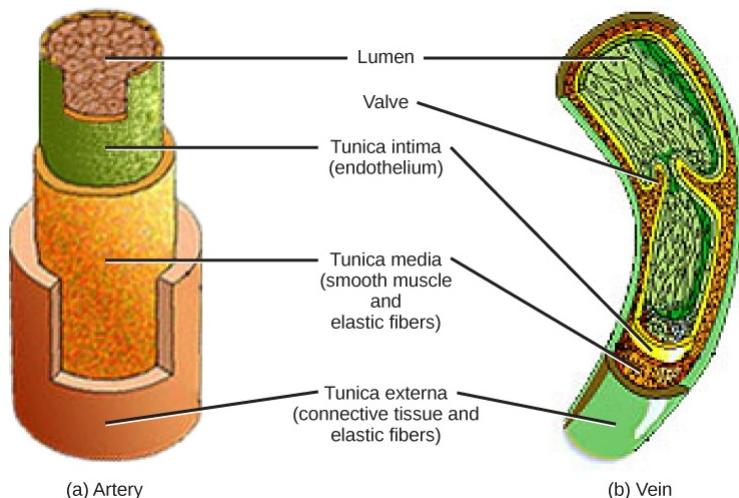


Arterioles diverge into capillary beds. **Capillary beds** contain a large number (10 to 100) of **capillaries** that branch among the cells and tissues

of the body. Capillaries are narrow-diameter tubes that can fit red blood cells through in single file and are the sites for the exchange of nutrients, waste, and oxygen with tissues at the cellular level. Fluid also crosses into the interstitial space from the capillaries. The capillaries converge again into **venules** that connect to minor veins that finally connect to major veins that take blood high in carbon dioxide back to the heart. **Veins** are blood vessels that bring blood back to the heart. The major veins drain blood from the same organs and limbs that the major arteries supply. Fluid is also brought back to the heart via the lymphatic system.

The structure of the different types of blood vessels reflects their function or layers. There are three distinct layers, or tunics, that form the walls of blood vessels ([\[link\]](#)). The first tunic is a smooth, inner lining of endothelial cells that are in contact with the red blood cells. The endothelial tunic is continuous with the endocardium of the heart. In capillaries, this single layer of cells is the location of diffusion of oxygen and carbon dioxide between the endothelial cells and red blood cells, as well as the exchange site via endocytosis and exocytosis. The movement of materials at the site of capillaries is regulated by **vasoconstriction**, narrowing of the blood vessels, and **vasodilation**, widening of the blood vessels; this is important in the overall regulation of blood pressure.

Veins and arteries both have two further tunics that surround the endothelium: the middle tunic is composed of smooth muscle and the outermost layer is connective tissue (collagen and elastic fibers). The elastic connective tissue stretches and supports the blood vessels, and the smooth muscle layer helps regulate blood flow by altering vascular resistance through vasoconstriction and vasodilation. The arteries have thicker smooth muscle and connective tissue than the veins to accommodate the higher pressure and speed of freshly pumped blood. The veins are thinner walled as the pressure and rate of flow are much lower. In addition, veins are structurally different than arteries in that veins have valves to prevent the backflow of blood. Because veins have to work against gravity to get blood back to the heart, contraction of skeletal muscle assists with the flow of blood back to the heart.



Section Summary

The heart muscle pumps blood through three divisions of the circulatory system: coronary, pulmonary, and systemic. There is one atrium and one ventricle on the right side and one atrium and one ventricle on the left side. The pumping of the heart is a function of cardiomyocytes, distinctive muscle cells that are striated like skeletal muscle but pump rhythmically and involuntarily like smooth muscle. The internal pacemaker starts at the sinoatrial node, which is located near the wall of the right atrium. Electrical charges pulse from the SA node causing the two atria to contract in unison; then the pulse reaches the atrioventricular node between the right atrium and right ventricle. A pause in the electric signal allows the atria to empty completely into the ventricles before the ventricles pump out the blood. The blood from the heart is carried through the body by a complex network of blood vessels; arteries take blood away from the heart, and veins bring blood back to the heart.

Art Connections

[link] Which of the following statements about the circulatory system is false?

1. Blood in the pulmonary vein is deoxygenated.
 2. Blood in the inferior vena cava is deoxygenated.
 3. Blood in the pulmonary artery is deoxygenated.
 4. Blood in the aorta is oxygenated.
-

[\[link\]](#) C

[\[link\]](#) Which of the following statements about the heart is false?

1. The mitral valve separates the left ventricle from the left atrium.
 2. Blood travels through the bicuspid valve to the left atrium.
 3. Both the aortic and the pulmonary valves are semilunar valves.
 4. The mitral valve is an atrioventricular valve.
-

[\[link\]](#) B

Review Questions

The heart's internal pacemaker beats by:

1. an internal implant that sends an electrical impulse through the heart
 2. the excitation of cardiac muscle cells at the sinoatrial node followed by the atrioventricular node
 3. the excitation of cardiac muscle cells at the atrioventricular node followed by the sinoatrial node
 4. the action of the sinus
-

B

During the systolic phase of the cardiac cycle, the heart is ____.

1. contracting
 2. relaxing
 3. contracting and relaxing
 4. filling with blood
-

A

Cardiomyocytes are similar to skeletal muscle because:

1. they beat involuntarily

-
- 2. they are used for weight lifting
 - 3. they pulse rhythmically
 - 4. they are striated

D

How do arteries differ from veins?

- 1. Arteries have thicker smooth muscle layers to accommodate the changes in pressure from the heart.
- 2. Arteries carry blood.
- 3. Arteries have thinner smooth muscle layers and valves and move blood by the action of skeletal muscle.
- 4. Arteries are thin walled and are used for gas exchange.

A

Free Response

Describe the cardiac cycle.

The heart receives an electrical signal from the

sinoatrial node triggering the cardiac muscle cells in the atria to contract. The signal pauses at the atrioventricular node before spreading to the walls of the ventricles so the blood is pumped through the body. This is the systolic phase. The heart then relaxes in the diastole and fills again with blood.

What happens in capillaries?

The capillaries basically exchange materials with their surroundings. Their walls are very thin and are made of one or two layers of cells, where gases, nutrients, and waste are diffused. They are distributed as beds, complex networks that link arteries as well as veins.

Glossary

angina

pain caused by partial blockage of the coronary arteries by the buildup of plaque and lack of oxygen to the heart muscle

aorta

major artery of the body that takes blood away from the heart

arteriole

small vessel that connects an artery to a capillary bed

artery

blood vessel that takes blood away from the heart

atherosclerosis

buildup of fatty plaques in the coronary arteries in the heart

atrioventricular valve

one-way membranous flap of connective tissue between the atrium and the ventricle in the right side of the heart; also known as tricuspid valve

bicuspid valve

(also, mitral valve; left atrioventricular valve)
one-way membranous flap between the atrium and the ventricle in the left side of the heart

capillary

smallest blood vessel that allows the passage of individual blood cells and the site of diffusion of oxygen and nutrient exchange

capillary bed

large number of capillaries that converge to take blood to a particular organ or tissue

cardiac cycle

filling and emptying the heart of blood by electrical signals that cause the heart muscles to contract and relax

cardiomyocyte

specialized heart muscle cell that is striated but contracts involuntarily like smooth muscle

coronary artery

vessel that supplies the heart tissue with blood

coronary vein

vessel that takes blood away from the heart tissue back to the chambers in the heart

diastole

relaxation phase of the cardiac cycle when the heart is relaxed and the ventricles are filling with blood

electrocardiogram (ECG)

recording of the electrical impulses of the cardiac muscle

endocardium

innermost layer of tissue in the heart

epicardium

outermost tissue layer of the heart

inferior vena cava

drains blood from the veins that come from the lower organs and the legs

myocardial infarction

(also, heart attack) complete blockage of the coronary arteries and death of the cardiac muscle tissue

myocardium

heart muscle cells that make up the middle layer and the bulk of the heart wall

pericardium

membrane layer protecting the heart; also part of the epicardium

semilunar valve

membranous flap of connective tissue between the aorta and a ventricle of the heart (the aortic or pulmonary semilunar valves)

sinoatrial (SA) node

the heart's internal pacemaker; located near the wall of the right atrium

superior vena cava

drains blood from the jugular vein that comes from the brain and from the veins that come from the arms

systole

contraction phase of cardiac cycle when the ventricles are pumping blood into the arteries

tricuspid valve

one-way membranous flap of connective tissue between the atrium and the ventricle in the right side of the heart; also known as atrioventricular valve

vasoconstriction

narrowing of a blood vessel

vasodilation

widening of a blood vessel

vein

blood vessel that brings blood back to the heart

vena cava

major vein of the body returning blood from the upper and lower parts of the body; see the superior vena cava and inferior vena cava

venule

blood vessel that connects a capillary bed to a vein

Blood Flow and Blood Pressure Regulation

By the end of this section, you will be able to:

- Describe the system of blood flow through the body
- Describe how blood pressure is regulated

Blood pressure (BP) is the pressure exerted by blood on the walls of a blood vessel that helps to push blood through the body. Systolic blood pressure measures the amount of pressure that blood exerts on vessels while the heart is beating. The optimal systolic blood pressure is 120 mmHg. Diastolic blood pressure measures the pressure in the vessels between heartbeats. The optimal diastolic blood pressure is 80 mmHg. Many factors can affect blood pressure, such as hormones, stress, exercise, eating, sitting, and standing. Blood flow through the body is regulated by the size of blood vessels, by the action of smooth muscle, by one-way valves, and by the fluid pressure of the blood itself. Fluid from the capillaries moves into the interstitial space and lymph capillaries by diffusion down a pressure gradient and also by osmosis. Out of 7,200 liters of fluid pumped by the average heart in a day, over 1,500 liters is filtered. (credit: modification of work by NCI, NIH)

How Blood Flows Through the Body

Blood is pushed through the body by the action of the pumping heart. With each rhythmic pump, blood is pushed under high pressure and velocity away from the heart, initially along the main artery, the aorta. In the aorta, the blood travels at 30 cm/sec. As blood moves into the arteries, arterioles, and ultimately to the capillary beds, the rate of movement slows dramatically to about 0.026 cm/sec, one-thousand times slower than the rate of movement in the aorta. While the diameter of each individual arteriole and capillary is far narrower than the diameter of the aorta, and according to the law of continuity, fluid should travel faster through a narrower diameter tube, the rate is actually slower due to the overall diameter of all the combined capillaries being far greater than the diameter of the individual aorta.

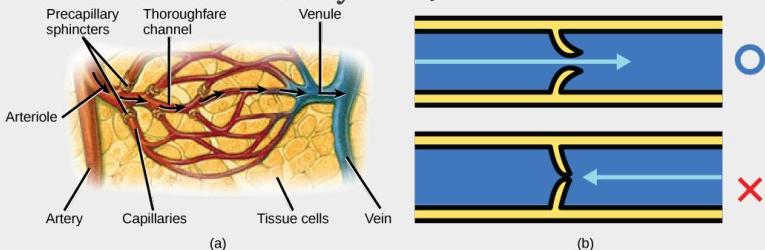
The slow rate of travel through the capillary beds, which reach almost every cell in the body, assists with gas and nutrient exchange and also promotes the diffusion of fluid into the interstitial space. After the blood has passed through the capillary beds to the venules, veins, and finally to the main venae cavae, the rate of flow increases again but is still much slower than the initial rate in the aorta. Blood primarily moves in the veins by the rhythmic movement of smooth muscle in the vessel wall and by the action of the skeletal muscle as the body moves. Because most veins must move blood against the pull of gravity, blood is prevented from flowing

backward in the veins by one-way valves. Because skeletal muscle contraction aids in venous blood flow, it is important to get up and move frequently after long periods of sitting so that blood will not pool in the extremities.

Blood flow through the capillary beds is regulated depending on the body's needs and is directed by nerve and hormone signals. For example, after a large meal, most of the blood is diverted to the stomach by vasodilation of vessels of the digestive system and vasoconstriction of other vessels. During exercise, blood is diverted to the skeletal muscles through vasodilation while blood to the digestive system would be lessened through vasoconstriction. The blood entering some capillary beds is controlled by small muscles, called precapillary sphincters, illustrated in [\[link\]](#). If the sphincters are open, the blood will flow into the associated branches of the capillary blood. If all of the sphincters are closed, then the blood will flow directly from the arteriole to the venule through the thoroughfare channel (see [\[link\]](#)). These muscles allow the body to precisely control when capillary beds receive blood flow. At any given moment only about 5-10% of our capillary beds actually have blood flowing through them.

Art Connection

(a) Precapillary sphincters are rings of smooth muscle that regulate the flow of blood through capillaries; they help control the location of blood flow to where it is needed. (b) Valves in the veins prevent blood from moving backward. (credit a: modification of work by NCI)



Varicose veins are veins that become enlarged because the valves no longer close properly, allowing blood to flow backward. Varicose veins are often most prominent on the legs. Why do you think this is the case?

Link to Learning

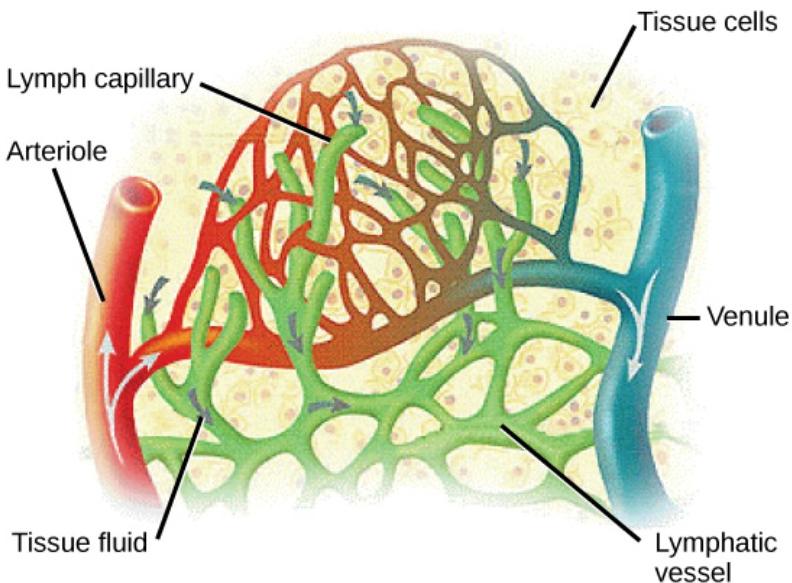


See the circulatory system's blood flow.

<https://www.openstaxcollege.org/l/circulation>

Proteins and other large solutes cannot leave the capillaries. The loss of the watery plasma creates a hyperosmotic solution within the capillaries, especially near the venules. This causes about 85% of the plasma that leaves the capillaries to eventually diffuses back into the capillaries near the venules. The remaining 15% of blood plasma drains out from the interstitial fluid into nearby lymphatic vessels ([\[link\]](#)). The fluid in the lymph is similar in composition to the interstitial fluid. The lymph fluid passes through lymph nodes before it returns to the heart via the vena cava. **Lymph nodes** are specialized organs that filter the lymph by percolation through a maze of connective tissue filled with white blood cells. The white blood cells remove infectious agents, such as bacteria and viruses, to clean the lymph before it returns to the bloodstream. After it is cleaned, the lymph returns to the heart by the action of smooth muscle pumping, skeletal muscle action, and one-way valves joining the returning blood near the junction of the venae cavae entering the right atrium of the heart.

Lymph Capillaries in the Tissue Spaces



Evolution Connection

Vertebrate Diversity in Blood Circulation

Blood circulation has evolved differently in vertebrates and may show variation in different animals for the required amount of pressure, organ and vessel location, and organ size. Animals with long necks and those that live in cold environments have distinct blood pressure adaptations.

Long necked animals, such as giraffes, need to pump blood upward from the heart against gravity. The blood pressure required from the pumping of the left ventricle would be equivalent to 250 mm Hg (mm Hg = millimeters of mercury, a unit of

pressure) to reach the height of a giraffe's head, which is 2.5 meters higher than the heart.

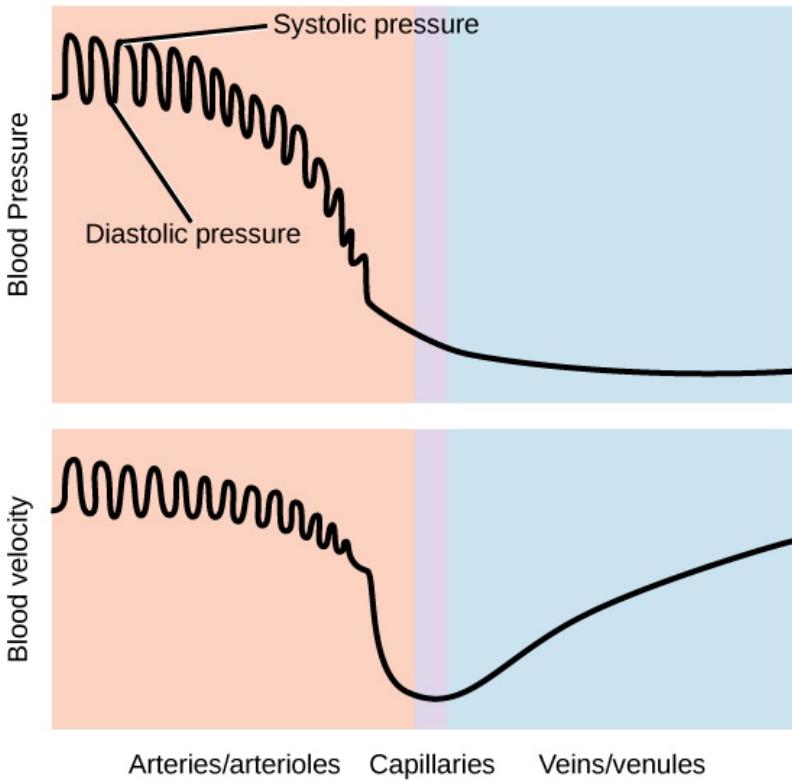
However, if checks and balances were not in place, this blood pressure would damage the giraffe's brain, particularly if it was bending down to drink. These checks and balances include valves and feedback mechanisms that reduce the rate of cardiac output. Long-necked dinosaurs such as the sauropods had to pump blood even higher, up to ten meters above the heart. This would have required a blood pressure of more than 600 mm Hg, which could only have been achieved by an enormous heart. Evidence for such an enormous heart does not exist and mechanisms to reduce the blood pressure required include the slowing of metabolism as these animals grew larger. It is likely that they did not routinely feed on tree tops but grazed on the ground.

Living in cold water, whales need to maintain the temperature in their blood. This is achieved by the veins and arteries being close together so that heat exchange can occur. This mechanism is called a countercurrent heat exchanger. The blood vessels and the whole body are also protected by thick layers of blubber to prevent heat loss. In land animals that live in cold environments, thick fur and hibernation are used to retain heat and slow metabolism.

Blood pressure is related to the blood velocity in the arteries and arterioles. In the capillaries and veins, the blood pressure continues to decrease but velocity increases.

Blood Pressure

The pressure of the blood flow in the body is produced by the hydrostatic pressure of the fluid (blood) against the walls of the blood vessels. Fluid will move from areas of high to low hydrostatic pressures. In the arteries, the hydrostatic pressure near the heart is very high and blood flows to the arterioles where the rate of flow is slowed by the narrow openings of the arterioles. During systole, when new blood is entering the arteries, the artery walls stretch to accommodate the increase of pressure of the extra blood; during diastole, the walls return to normal because of their elastic properties. The blood pressure of the systole phase and the diastole phase, graphed in [\[link\]](#), gives the two pressure readings for blood pressure. For example, 120/80 indicates a reading of 120 mm Hg during the systole and 80 mm Hg during diastole. Throughout the cardiac cycle, the blood continues to empty into the arterioles at a relatively even rate. This resistance to blood flow is called **peripheral resistance**.



Blood Pressure Regulation

Cardiac output is the volume of blood pumped by the heart in one minute. It is calculated by multiplying the number of heart contractions that occur per minute (heart rate) times the **stroke volume** (the volume of blood pumped into the aorta per contraction of the left ventricle). Therefore, cardiac output can be increased by increasing heart rate, as when exercising. However, cardiac output can also be increased by increasing stroke volume,

such as if the heart contracts with greater strength. Stroke volume can also be increased by speeding blood circulation through the body so that more blood enters the heart between contractions. During heavy exertion, the blood vessels relax and increase in diameter, offsetting the increased heart rate and ensuring adequate oxygenated blood gets to the muscles. Stress triggers a decrease in the diameter of the blood vessels, consequently increasing blood pressure. These changes can also be caused by nerve signals or hormones, and even standing up or lying down can have a great effect on blood pressure.

Section Summary

Blood primarily moves through the body by the rhythmic movement of smooth muscle in the vessel wall and by the action of the skeletal muscle as the body moves. Blood is prevented from flowing backward in the veins by one-way valves. Blood flow through the capillary beds is controlled by precapillary sphincters to increase and decrease flow depending on the body's needs and is directed by nerve and hormone signals. Lymph vessels take fluid that has leaked out of the blood to the lymph nodes where it is cleaned before returning to the heart. During systole, blood enters the arteries, and the artery walls stretch to accommodate the extra blood. During diastole, the artery walls return to normal. The blood pressure of the systole phase and

the diastole phase gives the two pressure readings for blood pressure.

Art Connections

[\[link\]](#) Varicose veins are veins that become enlarged because the valves no longer close properly, allowing blood to flow backward. Varicose veins are often most prominent on the legs. Why do you think this is the case?

[\[link\]](#) Blood in the legs is farthest away from the heart and has to flow up to reach it.

Review Questions

High blood pressure would be a result of _____.

1. a high cardiac output and high peripheral resistance
2. a high cardiac output and low peripheral resistance
3. a low cardiac output and high peripheral resistance

-
- 4. a low cardiac output and low peripheral resistance
-

A

Free Response

How does blood pressure change during heavy exercise?

The heart rate increases, which increases the hydrostatic pressure against the artery walls. At the same time, the arterioles dilate in response to the increased exercise, which reduces peripheral resistance.

Glossary

blood pressure (BP)

pressure of blood in the arteries that helps to push blood through the body

cardiac output

the volume of blood pumped by the heart in one minute as a product of heart rate

multiplied by stroke volume

lymph node

specialized organ that contains a large number of macrophages that clean the lymph before the fluid is returned to the heart

peripheral resistance

resistance of the artery and blood vessel walls to the pressure placed on them by the force of the heart pumping

precapillary sphincter

small muscle that controls blood circulation in the capillary beds

stroke volume >

- the volume of blood pumped into the aorta per contraction of the left ventricle

Systems of Gas Exchange

By the end of this section, you will be able to:

- Describe the passage of air from the outside environment to the lungs
- Explain how the lungs are protected from particulate matter

The primary function of the respiratory system is to deliver oxygen to the cells of the body's tissues and remove carbon dioxide, a cell waste product. The main structures of the human respiratory system are the nasal cavity, the trachea, and lungs.

All aerobic organisms require oxygen to carry out their metabolic functions. Along the evolutionary tree, different organisms have devised different means of obtaining oxygen from the surrounding atmosphere. The environment in which the animal lives greatly determines how an animal respires. The complexity of the respiratory system is correlated with the size of the organism. As animal size increases, diffusion distances increase and the ratio of surface area to volume drops. In unicellular organisms, diffusion across the cell membrane is sufficient for supplying oxygen to the cell ([\[link\]](#)). Diffusion is a slow, passive transport process. In order for diffusion to be a feasible means of providing oxygen to the cell, the rate of oxygen uptake must match the rate of diffusion across the membrane. In other words, if the cell were very

large or thick, diffusion would not be able to provide oxygen quickly enough to the inside of the cell. Therefore, dependence on diffusion as a means of obtaining oxygen and removing carbon dioxide remains feasible only for small organisms or those with highly-flattened bodies, such as many flatworms (*Platyhelminthes*). Larger organisms had to evolve specialized respiratory tissues, such as gills, lungs, and respiratory passages accompanied by complex circulatory systems, to transport oxygen throughout their entire body.

The cell of the unicellular algae *Ventricaria ventricosa* is one of the largest known, reaching one to five centimeters in diameter. Like all single-celled organisms, *V. ventricosa* exchanges gases across the cell membrane.



This flatworm's process of respiration works by diffusion across the outer membrane. (credit:

Stephen Childs)

Direct Diffusion

For small multicellular organisms, diffusion across the outer membrane is sufficient to meet their oxygen needs. Gas exchange by direct diffusion across surface membranes is efficient for organisms less than 1 mm in diameter. In simple organisms, such as cnidarians and flatworms, every cell in the body is close to the external environment. Their cells are kept moist and gases diffuse quickly via direct diffusion. Flatworms are small, literally flat worms, which ‘breathe’ through diffusion across the outer membrane ([\[link\]](#)). The flat shape of these organisms increases the surface area for diffusion, ensuring that each cell within the body is close to the outer membrane surface and has access to oxygen. If the flatworm had a cylindrical body, then the cells in the center would not be able to get oxygen.



This common carp, like many other aquatic organisms, has gills that allow it to obtain oxygen from water. (credit: "Guitardude012"/Wikimedia Commons) As water flows over the gills, oxygen is transferred to blood via the veins. (credit "fish": modification of work by Duane Raver, NOAA)

Skin and Gills

Earthworms and amphibians use their skin (integument) as a respiratory organ. A dense network of capillaries lies just below the skin and facilitates gas exchange between the external environment and the circulatory system. The respiratory surface must be kept moist in order for the gases to dissolve and diffuse across cell membranes.

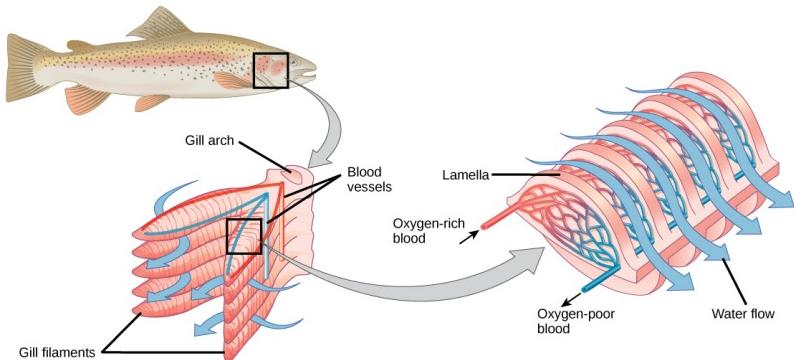
Organisms that live in water need to obtain oxygen from the water. Oxygen dissolves in water but at a

lower concentration than in the atmosphere. The atmosphere has roughly 21 percent oxygen. In water, the oxygen concentration is much smaller than that. Fish and many other aquatic organisms have evolved gills to take up the dissolved oxygen from water ([\[link\]](#)). Gills are thin tissue filaments that are highly branched and folded. When water passes over the gills, the dissolved oxygen in water rapidly diffuses across the gills into the bloodstream. The circulatory system can then carry the oxygenated blood to the other parts of the body. In animals that contain coelomic fluid instead of blood, oxygen diffuses across the gill surfaces into the coelomic fluid. Gills are found in mollusks, annelids, and crustaceans.



The folded surfaces of the gills provide a large surface area to ensure that the fish gets sufficient

oxygen. Diffusion is a process in which material travels from regions of high concentration to low concentration until equilibrium is reached. In this case, blood with a low concentration of oxygen molecules circulates through the gills. The concentration of oxygen molecules in water is higher than the concentration of oxygen molecules in gills. As a result, oxygen molecules diffuse from water (high concentration) to blood (low concentration), as shown in [\[link\]](#). Similarly, carbon dioxide molecules in the blood diffuse from the blood (high concentration) to water (low concentration).



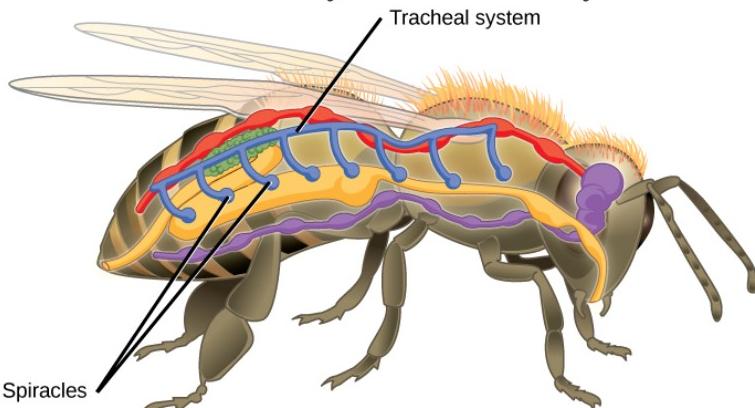
Insects perform respiration via a tracheal system.

Tracheal Systems

Insect respiration is independent of its circulatory system; therefore, the blood does not play a direct role in oxygen transport. Insects have a highly specialized type of respiratory system called the tracheal system, which consists of a network of small tubes that carries oxygen to the entire body.

The tracheal system is the most direct and efficient respiratory system in active animals. The tubes in the tracheal system are made of a polymeric material called chitin.

Insect bodies have openings, called spiracles, along the thorax and abdomen. These openings connect to the tubular network, allowing oxygen to pass into the body ([\[link\]](#)) and regulating the diffusion of CO₂ and water vapor. Air enters and leaves the tracheal system through the spiracles. Some insects can ventilate the tracheal system with body movements.



The trachea and bronchi are made of incomplete rings of cartilage. (credit: modification of work by Gray's Anatomy) The trachea bifurcates into the right and left bronchi in the lungs. The right lung is made of three lobes and is larger. To accommodate the heart, the left lung is smaller and has only two lobes. Terminal bronchioles are connected by respiratory bronchioles to alveolar ducts and alveolar sacs. Each alveolar sac contains 20 to 30 spherical alveoli and has the appearance of a bunch

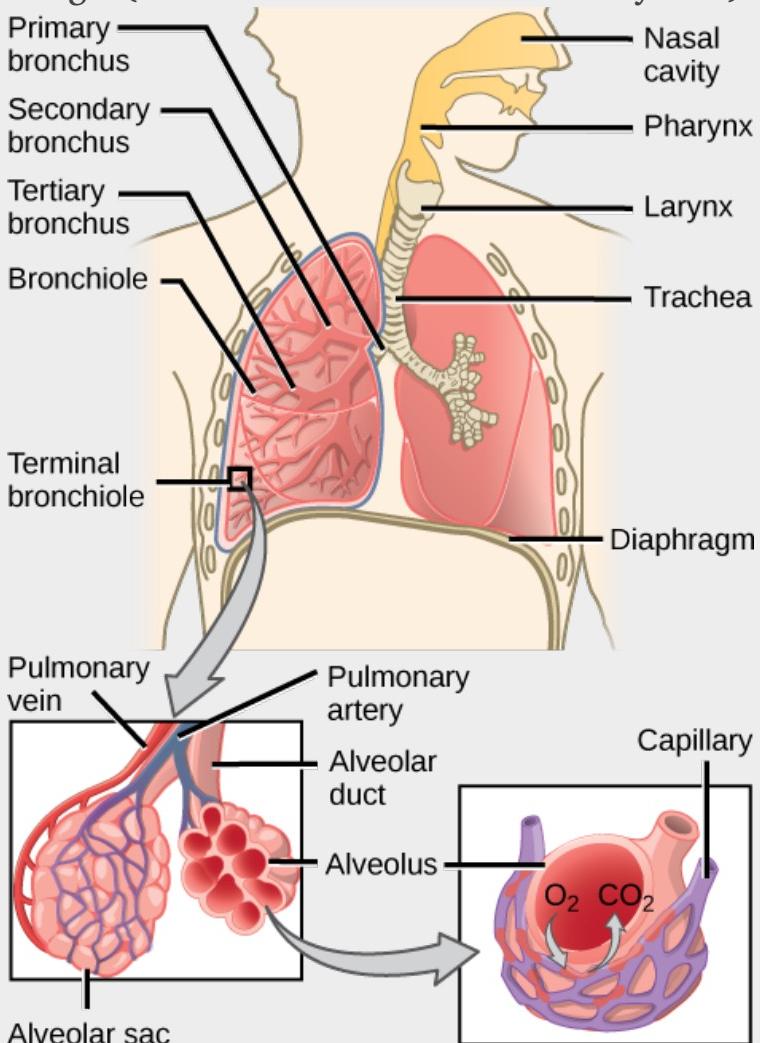
of grapes. Air flows into the atrium of the alveolar sac, then circulates into alveoli where gas exchange occurs with the capillaries. Mucous glands secrete mucous into the airways, keeping them moist and flexible. (credit: modification of work by Mariana Ruiz Villareal)

Mammalian Systems

In mammals, pulmonary ventilation occurs via inhalation (breathing). During inhalation, air enters the body through the **nasal cavity** located just inside the nose ([\[link\]](#)). As air passes through the nasal cavity, the air is warmed to body temperature and humidified. The respiratory tract is coated with mucus to seal the tissues from direct contact with air. Mucus is high in water. As air crosses these surfaces of the mucous membranes, it picks up water. These processes help equilibrate the air to the body conditions, reducing any damage that cold, dry air can cause. Particulate matter that is floating in the air is removed in the nasal passages via mucus and cilia. The processes of warming, humidifying, and removing particles are important protective mechanisms that prevent damage to the trachea and lungs. Thus, inhalation serves several purposes in addition to bringing oxygen into the respiratory system.

Art Connection

Air enters the respiratory system through the nasal cavity and pharynx, and then passes through the trachea and into the bronchi, which bring air into the lungs. (credit: modification of work by NCI)

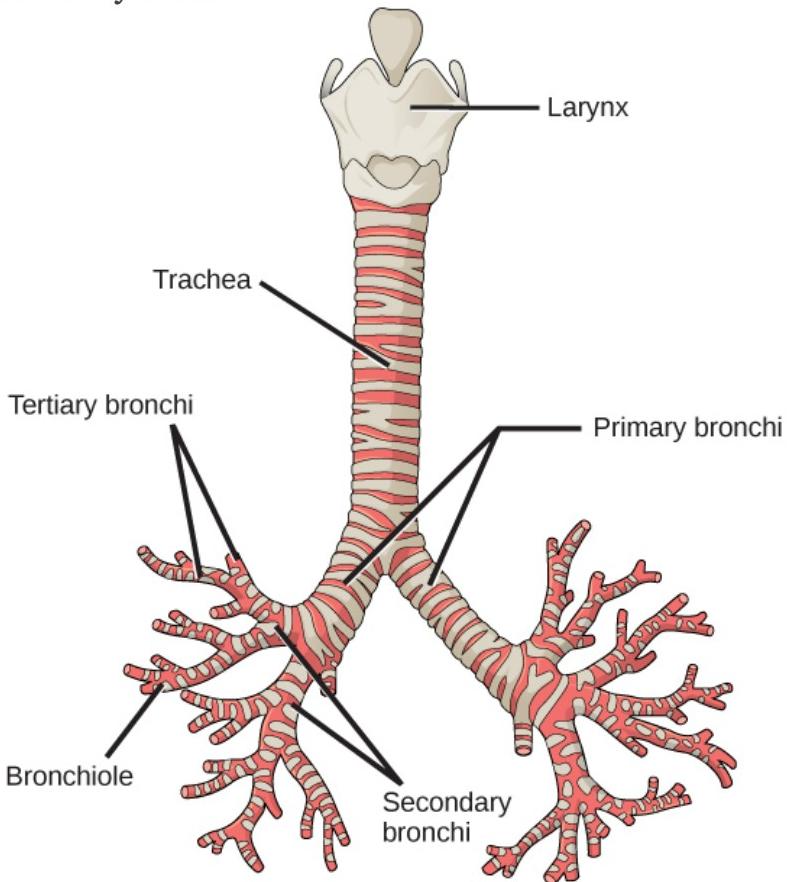


Which of the following statements about the mammalian respiratory system is false?

1. When we breathe in, air travels from the pharynx to the trachea.
2. The bronchioles branch into bronchi.
3. Alveolar ducts connect to alveolar sacs.
4. Gas exchange between the lung and blood takes place in the alveolus.

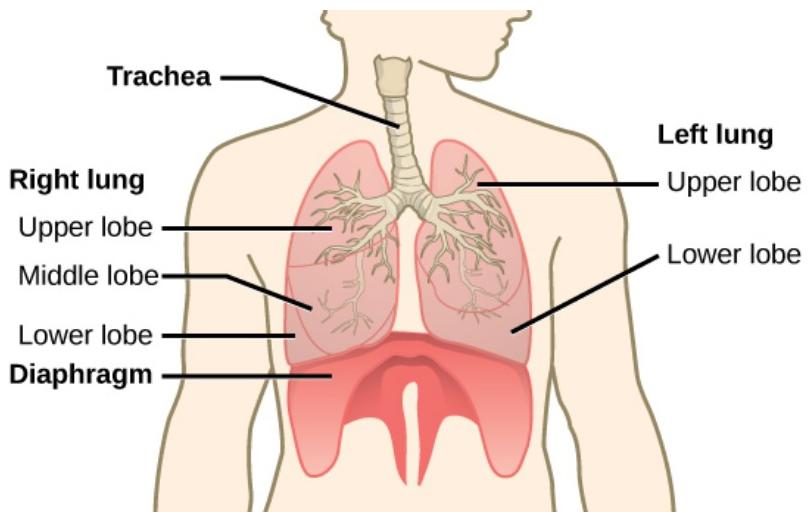
From the nasal cavity, air passes through the **pharynx** (throat) and the **larynx** (voice box), as it makes its way to the **trachea** ([\[link\]](#)). The main function of the trachea is to funnel the inhaled air to the lungs and the exhaled air back out of the body. The human trachea is a cylinder about 10 to 12 cm long and 2 cm in diameter that sits in front of the esophagus and extends from the larynx into the chest cavity where it divides into the two primary bronchi at the mid thorax. It is made of incomplete rings of hyaline cartilage and smooth muscle ([\[link\]](#)). The trachea is lined with mucus-producing goblet cells and ciliated epithelia. The cilia propel foreign particles trapped in the mucus toward the pharynx. The cartilage provides strength and support to the trachea to keep the passage open. The smooth muscle can contract, decreasing the trachea's diameter, which causes expired air to rush upwards from the lungs at a great force. The forced exhalation helps expel mucus when we cough. Smooth muscle can contract or relax, depending on stimuli from the external environment or the body's

nervous system.



Lungs: Bronchi and Alveoli

The end of the trachea bifurcates (divides) to the right and left lungs. The lungs are not identical. The right lung is larger and contains three lobes, whereas the smaller left lung contains two lobes ([\[link\]](#)). The muscular **diaphragm**, which facilitates breathing, is inferior to (below) the lungs and marks the end of the thoracic cavity.

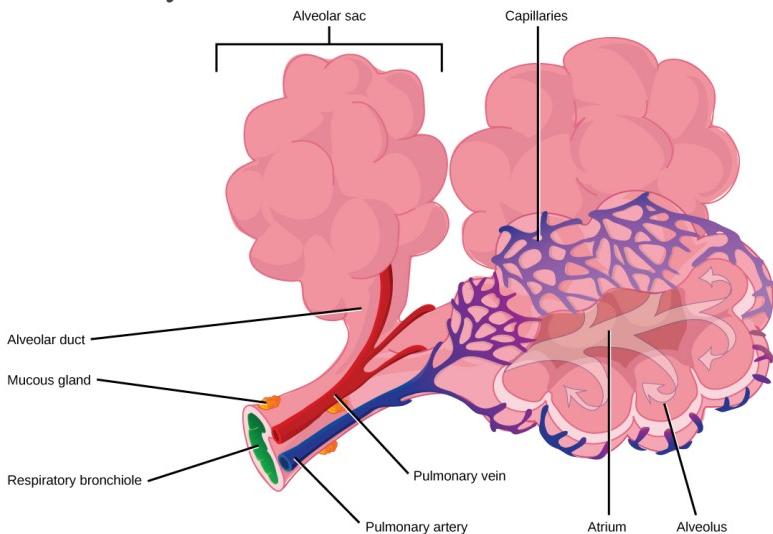


In the lungs, air is diverted into smaller and smaller passages, or **bronchi**. Air enters the lungs through the two **primary (main) bronchi** (singular: bronchus). Each bronchus divides into secondary bronchi, then into tertiary bronchi, which in turn divide, creating smaller and smaller diameter **bronchioles** as they split and spread through the lung. Like the trachea, the bronchi are made of cartilage and smooth muscle. At the bronchioles, the cartilage is replaced with elastic fibers. Bronchi are innervated by nerves of both the parasympathetic and sympathetic nervous systems that control muscle contraction (parasympathetic) or relaxation (sympathetic) in the bronchi and bronchioles, depending on the nervous system's cues. In humans, bronchioles with a diameter smaller than 0.5 mm are the **respiratory bronchioles**. They lack cartilage and therefore rely on inhaled air to support their shape. As the passageways decrease in

diameter, the relative amount of smooth muscle increases.

The **terminal bronchioles** subdivide into microscopic branches called respiratory bronchioles. The respiratory bronchioles subdivide into several alveolar ducts. Numerous alveoli and alveolar sacs surround the alveolar ducts. The alveolar sacs resemble bunches of grapes tethered to the end of the bronchioles ([\[link\]](#)). In the acinar region, the **alveolar ducts** are attached to the end of each bronchiole. At the end of each duct are approximately 100 **alveolar sacs**, each containing 20 to 30 **alveoli** that are 200 to 300 microns in diameter. Gas exchange occurs only in alveoli. Alveoli are made of thin-walled parenchymal cells, typically one-cell thick, that look like tiny bubbles within the sacs. Alveoli are in direct contact with capillaries (one-cell thick) of the circulatory system. Such intimate contact ensures that oxygen will diffuse from alveoli into the blood and be distributed to the cells of the body. In addition, the carbon dioxide that was produced by cells as a waste product will diffuse from the blood into alveoli to be exhaled. The anatomical arrangement of capillaries and alveoli emphasizes the structural and functional relationship of the respiratory and circulatory systems. Because there are so many alveoli (~300 million per lung) within each alveolar sac and so many sacs at the end of each alveolar duct, the lungs have a sponge-like consistency. This

organization produces a very large surface area that is available for gas exchange. The surface area of alveoli in the lungs is approximately 75 m². This large surface area, combined with the thin-walled nature of the alveolar parenchymal cells, allows gases to easily diffuse across the cells.



Link to Learning



Watch the following video to review the respiratory system.

The bronchi and bronchioles contain cilia that help move mucus and other particles out of the lungs.
(credit: Louisa Howard, modification of work by Dartmouth Electron Microscope Facility)

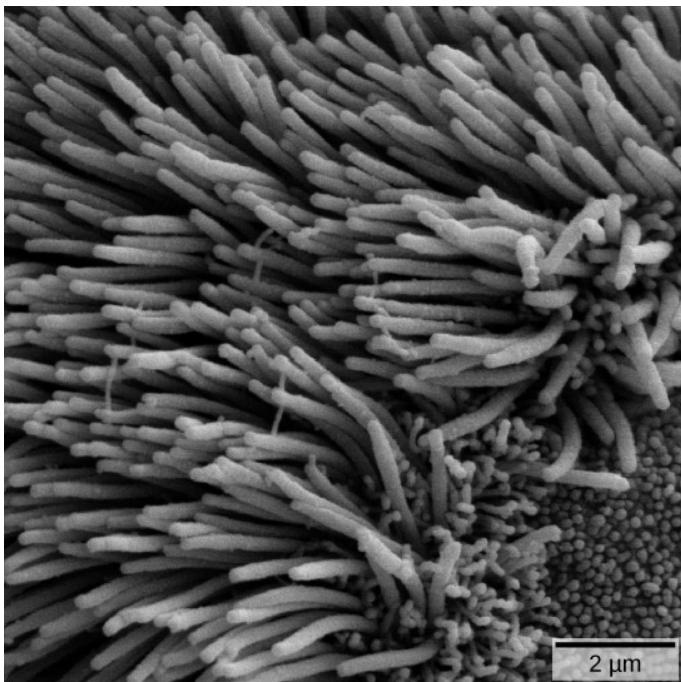
Protective Mechanisms

The air that organisms breathe contains **particulate matter** such as dust, dirt, viral particles, and bacteria that can damage the lungs or trigger allergic immune responses. The respiratory system contains several protective mechanisms to avoid problems or tissue damage. In the nasal cavity, hairs and mucus trap small particles, viruses, bacteria, dust, and dirt to prevent their entry.

If particulates do make it beyond the nose, or enter through the mouth, the bronchi and bronchioles of the lungs also contain several protective devices. The lungs produce **mucus**—a sticky substance made of **mucin**, a complex glycoprotein, as well as salts and water—that traps particulates. The bronchi and bronchioles contain cilia, small hair-like projections that line the walls of the bronchi and bronchioles ([\[link\]](#)). These cilia beat in unison and move mucus and particles out of the bronchi and bronchioles

back up to the throat where it is swallowed and eliminated via the esophagus.

In humans, for example, tar and other substances in cigarette smoke destroy or paralyze the cilia, making the removal of particles more difficult. In addition, smoking causes the lungs to produce more mucus, which the damaged cilia are not able to move. This causes a persistent cough, as the lungs try to rid themselves of particulate matter, and makes smokers more susceptible to respiratory ailments.



Section Summary

Animal respiratory systems are designed to facilitate gas exchange. In mammals, air is warmed and humidified in the nasal cavity. Air then travels down the pharynx, through the trachea, and into the lungs. In the lungs, air passes through the branching bronchi, reaching the respiratory bronchioles, which house the first site of gas exchange. The respiratory bronchioles open into the alveolar ducts, alveolar sacs, and alveoli. Because there are so many alveoli and alveolar sacs in the lung, the surface area for gas exchange is very large. Several protective mechanisms are in place to prevent damage or infection. These include the hair and mucus in the nasal cavity that trap dust, dirt, and other particulate matter before they can enter the system. In the lungs, particles are trapped in a mucus layer and transported via cilia up to the esophageal opening at the top of the trachea to be swallowed.

[\[link\]](#) Which of the following statements about the mammalian respiratory system is false?

1. When we breathe in, air travels from the pharynx to the trachea.
 2. The bronchioles branch into bronchi.
 3. Alveolar ducts connect to alveolar sacs.
 4. Gas exchange between the lung and blood takes place in the alveolus.
-

[link] B

Review Questions

The respiratory system _____.

1. provides body tissues with oxygen
 2. provides body tissues with oxygen and carbon dioxide
 3. establishes how many breaths are taken per minute
 4. provides the body with carbon dioxide
-

A

Air is warmed and humidified in the nasal passages. This helps to _____.

1. ward off infection
 2. decrease sensitivity during breathing
 3. prevent damage to the lungs
 4. all of the above
-

C

Which is the order of airflow during inhalation?

1. nasal cavity, trachea, larynx, bronchi, bronchioles, alveoli
 2. nasal cavity, larynx, trachea, bronchi, bronchioles, alveoli
 3. nasal cavity, larynx, trachea, bronchioles, bronchi, alveoli
 4. nasal cavity, trachea, larynx, bronchi, bronchioles, alveoli
-

B

Free Response

Describe the function of these terms and describe where they are located: main bronchus, trachea, alveoli, and acinus.

The main bronchus is the conduit in the lung that funnels air to the airways where gas exchange occurs. The main bronchus attaches the lungs to the very end of the trachea where it bifurcates. The trachea is the cartilaginous structure that extends from the pharynx to the primary bronchi. It serves to funnel air to the

lungs. The alveoli are the sites of gas exchange; they are located at the terminal regions of the lung and are attached to the respiratory bronchioles. The acinus is the structure in the lung where gas exchange occurs.

How does the structure of alveoli maximize gas exchange?

The sac-like structure of the alveoli increases their surface area. In addition, the alveoli are made of thin-walled parenchymal cells. These features allow gases to easily diffuse across the cells.

Glossary

alveolar duct

duct that extends from the terminal bronchiole to the alveolar sac

alveolar sac

structure consisting of two or more alveoli that share a common opening

alveolus

(plural: alveoli) (also, air sac) terminal region of the lung where gas exchange occurs

bronchus

(plural: bronchi) smaller branch of cartilaginous tissue that stems off of the trachea; air is funneled through the bronchi to the region where gas exchange occurs in alveoli

bronchiole

airway that extends from the main tertiary bronchi to the alveolar sac

diaphragm

domed-shaped skeletal muscle located under lungs that separates the thoracic cavity from the abdominal cavity

larynx

voice box, a short passageway connecting the pharynx and the trachea

mucin

complex glycoprotein found in mucus

mucus

sticky protein-containing fluid secretion in the lung that traps particulate matter to be expelled from the body

nasal cavity

opening of the respiratory system to the outside environment

particulate matter

small particle such as dust, dirt, viral particles, and bacteria that are in the air

pharynx

throat; a tube that starts in the internal nares and runs partway down the neck, where it opens into the esophagus and the larynx

primary bronchus

(also, main bronchus) region of the airway within the lung that attaches to the trachea and bifurcates to each lung where it branches into secondary bronchi

respiratory bronchiole

terminal portion of the bronchiole tree that is attached to the terminal bronchioles and alveoli ducts, alveolar sacs, and alveoli

terminal bronchiole

region of bronchiole that attaches to the respiratory bronchioles

trachea

cartilaginous tube that transports air from the larynx to the primary bronchi

Gas Exchange across Respiratory Surfaces

By the end of this section, you will be able to do the following:

- Name and describe lung volumes and capacities
- Understand how gas pressure influences how gases move into and out of the body

The structure of the lung maximizes its surface area to increase gas diffusion. Because of the enormous number of alveoli (approximately 300 million in each human lung), the surface area of the lung is very large (75 m^2). Having such a large surface area increases the amount of gas that can diffuse into and out of the lungs.

Basic Principles of Gas Exchange

Gas exchange during respiration occurs primarily through diffusion. Diffusion is a process in which transport is driven by a concentration gradient. Gas molecules move from a region of high concentration to a region of low concentration. Blood that is low in oxygen concentration and high in carbon dioxide concentration undergoes gas exchange with air in the lungs. The air in the lungs has a higher concentration of oxygen than that of oxygen-depleted blood and a lower concentration of carbon dioxide. This concentration gradient allows for gas

exchange during respiration.

Partial pressure is a measure of the concentration of the individual components in a mixture of gases. The total pressure exerted by the mixture is the sum of the partial pressures of the components in the mixture. The rate of diffusion of a gas is proportional to its partial pressure within the total gas mixture. This concept is discussed further in detail below.

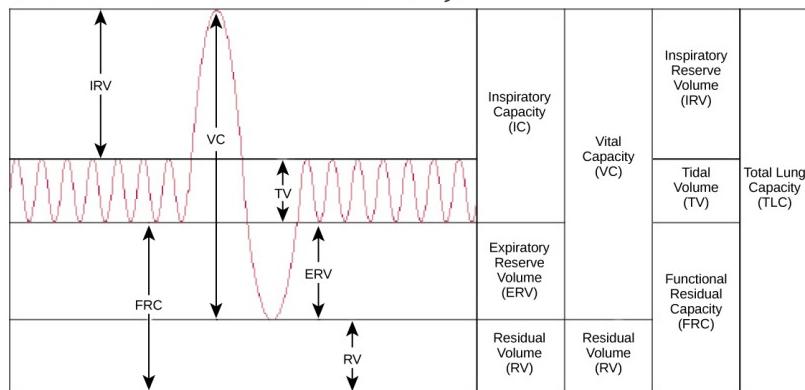
Human lung volumes and capacities are shown. The total lung capacity of the adult male is six liters. Tidal volume is the volume of air inhaled in a single, normal breath. Inspiratory capacity is the amount of air taken in during a deep breath, and residual volume is the amount of air left in the lungs after forceful respiration.

Lung Volumes and Capacities

Different animals have different lung capacities based on their activities. Cheetahs have evolved a much higher lung capacity than humans; it helps provide oxygen to all the muscles in the body and allows them to run very fast. Elephants also have a high lung capacity. In this case, it is not because they run fast but because they have a large body and must be able to take up oxygen in accordance with their body size.

Human lung size is determined by genetics, sex, and

height. At maximal capacity, an average lung can hold almost six liters of air, but lungs do not usually operate at maximal capacity. Air in the lungs is measured in terms of **lung volumes** and **lung capacities** ([\[link\]](#) and [\[link\]](#)). Volume measures the amount of air for one function (such as inhalation or exhalation). Capacity is any two or more volumes (for example, how much can be inhaled from the end of a maximal exhalation).



Lung Volumes and Capacities (Avg Adult Male)

Volume/Capacity

Definition

Volume (liters)

Equations

Tidal volume (TV)	Amount of air inhaled during a normal breath	0.5	-	
Expiratory reserve volume (ERV)	Amount of air that can be exhaled after a normal exhalation	1.2	-	
Inspiratory reserve volume (IRV)	Amount of air that can be further inhaled after a normal inhalation	3.1	-	
Residual volume (RV)	Air left in the lungs after a forced exhalation	1.2	-	
Vital capacity (VC)	Maximum amount of air that can be moved in or out of the lungs in a single respiratory cycle	4.8	ERV + TV + IRV	

Inspiratory capacity (IC)	Volume of air that can be inhaled in addition to a normal exhalation	3.6	TV + IRV
Functional residual capacity (FRC)	Volume of air remaining after a normal exhalation	2.4	ERV + RV
Total lung capacity (TLC)	Total volume of air in the lungs after a maximal inspiration	6.0	RV + ERV + TV + IRV
Forced expiratory volume (FEV1)	How much air can be forced out of the lungs over a specific time period, usually one second	~4.1 to 5.5	-

The volume in the lung can be divided into four units: tidal volume, expiratory reserve volume, inspiratory reserve volume, and residual volume.

Tidal volume (TV) measures the amount of air that is inspired and expired during a normal breath. On average, this volume is around one-half liter, which is a little less than the capacity of a 20-ounce drink bottle. The **expiratory reserve volume (ERV)** is the additional amount of air that can be exhaled after a normal exhalation. It is the reserve amount that can be exhaled beyond what is normal. Conversely, the **inspiratory reserve volume (IRV)** is the additional amount of air that can be inhaled after a normal inhalation. The **residual volume (RV)** is the amount of air that is left after expiratory reserve volume is exhaled. The lungs are never completely empty: There is always some air left in the lungs after a maximal exhalation. If this residual volume did not exist and the lungs emptied completely, the lung tissues would stick together and the energy necessary to reinflate the lung could be too great to overcome. Therefore, there is always some air remaining in the lungs. Residual volume is also important for preventing large fluctuations in respiratory gases (O_2 and CO_2). The residual volume is the only lung volume that cannot be measured directly because it is impossible to completely empty the lung of air. This volume can only be calculated rather than measured.

Capacities are measurements of two or more volumes. The **vital capacity (VC)** measures the maximum amount of air that can be inhaled or exhaled during a respiratory cycle. It is the sum of

the expiratory reserve volume, tidal volume, and inspiratory reserve volume. The **inspiratory capacity (IC)** is the amount of air that can be inhaled after the end of a normal expiration. It is, therefore, the sum of the tidal volume and inspiratory reserve volume. The **functional residual capacity (FRC)** includes the expiratory reserve volume and the residual volume. The FRC measures the amount of additional air that can be exhaled after a normal exhalation. Lastly, the **total lung capacity (TLC)** is a measurement of the total amount of air that the lung can hold. It is the sum of the residual volume, expiratory reserve volume, tidal volume, and inspiratory reserve volume.

Lung volumes are measured by a technique called **spirometry**. An important measurement taken during spirometry is the **forced expiratory volume (FEV)**, which measures how much air can be forced out of the lung over a specific period, usually one second (FEV1). In addition, the forced vital capacity (FVC), which is the total amount of air that can be forcibly exhaled, is measured. The ratio of these values (**FEV1/FVC ratio**) is used to diagnose lung diseases including asthma, emphysema, and fibrosis. If the FEV1/FVC ratio is high, the lungs are not compliant (meaning they are stiff and unable to bend properly), and the patient most likely has lung fibrosis. Patients exhale most of the lung volume very quickly. Conversely, when the FEV1/FVC ratio is low, there is resistance in the lung that is

characteristic of asthma. In this instance, it is hard for the patient to get the air out of his or her lungs, and it takes a long time to reach the maximal exhalation volume. In either case, breathing is difficult and complications arise.

Career Connection

Respiratory Therapist

Respiratory therapists or respiratory practitioners evaluate and treat patients with lung and cardiovascular diseases. They work as part of a medical team to develop treatment plans for patients. Respiratory therapists may treat premature babies with underdeveloped lungs, patients with chronic conditions such as asthma, or older patients suffering from lung disease such as emphysema and chronic obstructive pulmonary disease (COPD). They may operate advanced equipment such as compressed gas delivery systems, ventilators, blood gas analyzers, and resuscitators. Specialized programs to become a respiratory therapist generally lead to a bachelor's degree with a respiratory therapist specialty. Because of a growing aging population, career opportunities as a respiratory therapist are expected to remain strong.

Gas Pressure and Respiration

The respiratory process can be better understood by examining the properties of gases. Gases move freely, but gas particles are constantly hitting the walls of their vessel, thereby producing gas pressure.

Air is a mixture of gases, primarily nitrogen (N_2 ; 78.6 percent), oxygen (O_2 ; 20.9 percent), water vapor (H_2O ; 0.5 percent), and carbon dioxide (CO_2 ; 0.04 percent). Each gas component of that mixture exerts a pressure. The pressure for an individual gas in the mixture is the partial pressure of that gas. Approximately 21 percent of atmospheric gas is oxygen. Carbon dioxide, however, is found in relatively small amounts, 0.04 percent. The partial pressure for oxygen is much greater than that of carbon dioxide. The partial pressure of any gas can be calculated by:

$$P = (P_{atm}) \times (\text{percent content in mixture}).$$

P_{atm} , the atmospheric pressure, is the sum of all of the partial pressures of the atmospheric gases added together,

$$\begin{aligned} P_{atm} &= P_{N_2} + P_{O_2} + P_{H_2O} + P_{CO_2} \\ &= 760 \text{ mm Hg} \end{aligned}$$

$$\times (\text{percent content in mixture}).$$

The pressure of the atmosphere at sea level is 760 mm Hg. Therefore, the partial pressure of oxygen is:
 $P\text{ O}_2 = (760 \text{ mm Hg}) (0.21) = 160 \text{ mm Hg}$

and for carbon dioxide:

$$P\text{ CO}_2 = (760 \text{ mm Hg}) (0.0004) = 0.3 \text{ mm Hg}.$$

At high altitudes, P_{atm} decreases but concentration does not change; the partial pressure decrease is due to the reduction in P_{atm} .

When the air mixture reaches the lung, it has been humidified. The pressure of the water vapor in the lung does not change the pressure of the air, but it must be included in the partial pressure equation. For this calculation, the water pressure (47 mm Hg) is subtracted from the atmospheric pressure:

$$760 \text{ mm Hg} - 47 \text{ mm Hg} = 713 \text{ mm Hg}$$

and the partial pressure of oxygen is:

$$(760 \text{ mm Hg} - 47 \text{ mm Hg}) \times 0.21 = 150 \text{ mm Hg}.$$

These pressures determine the gas exchange, or the flow of gas, in the system. Oxygen and carbon dioxide will flow according to their pressure gradient from high to low. Therefore, understanding the partial pressure of each gas will aid in understanding how gases move in the respiratory system.

Gas Exchange across the Alveoli

In the body, oxygen is used by cells of the body's tissues and carbon dioxide is produced as a waste product. The ratio of carbon dioxide production to oxygen consumption is the **respiratory quotient (RQ)**. RQ varies between 0.7 and 1.0. If just glucose were used to fuel the body, the RQ would equal one. One mole of carbon dioxide would be produced for every mole of oxygen consumed. Glucose, however, is not the only fuel for the body. Protein and fat are also used as fuels for the body. Because of this, less carbon dioxide is produced than oxygen is consumed and the RQ is, on average, about 0.7 for fat and about 0.8 for protein.

The RQ is used to calculate the partial pressure of oxygen in the alveolar spaces within the lung, the **alveolar P O₂**. Above, the partial pressure of oxygen in the lungs was calculated to be 150 mm Hg. However, lungs never fully deflate with an exhalation; therefore, the inspired air mixes with this residual air and lowers the partial pressure of oxygen within the alveoli. This means that there is a lower concentration of oxygen in the lungs than is found in the air outside the body. Knowing the RQ, the partial pressure of oxygen in the alveoli can be calculated:

$$\text{alveolar P O}_2 = \text{inspired P O}_2 - (\text{alveolar P O}_2 \times \text{RQ})$$

With an RQ of 0.8 and a P CO₂ in the alveoli of 40 mm Hg, the alveolar P O₂ is equal to:

$$\text{alveolar P O}_2 = 150 \text{ mm Hg} - (40 \text{ mm Hg} \cdot 0.8) \\) = 100 \text{ mm Hg.}$$

Notice that this pressure is less than the external air. Therefore, the oxygen will flow from the inspired air in the lung (P O₂ = 150 mm Hg) into the bloodstream (P O₂ = 100 mm Hg) ([\[link\]](#)).

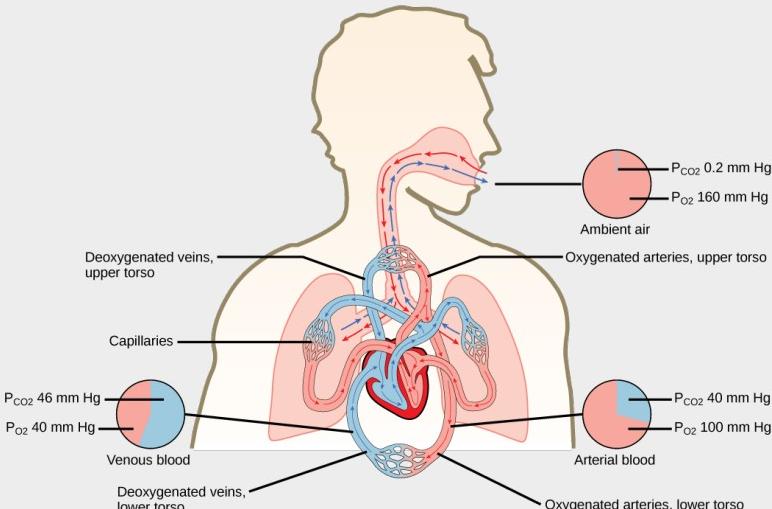
In the lungs, oxygen diffuses out of the alveoli and into the capillaries surrounding the alveoli. Oxygen (about 98 percent) binds reversibly to the respiratory pigment hemoglobin found in red blood cells (RBCs). RBCs carry oxygen to the tissues where oxygen dissociates from the hemoglobin and diffuses into the cells of the tissues. More specifically, alveolar P O₂ is higher in the alveoli (P ALVO₂ = 100 mm Hg) than blood P O₂ (40 mm Hg) in the capillaries. Because this pressure gradient exists, oxygen diffuses down its pressure gradient, moving out of the alveoli and entering the blood of the capillaries where O₂ binds to hemoglobin. At the same time, alveolar P CO₂ is lower P ALVO₂ = 40 mm Hg than blood P CO₂ = (45 mm Hg). CO₂ diffuses down its pressure gradient, moving out of the capillaries and entering the alveoli.

Oxygen and carbon dioxide move independently of each other; they diffuse down their own pressure gradients. As blood leaves the lungs through the

pulmonary veins, the **venous P O₂** = 100 mm Hg, whereas the **venous P CO₂** = 40 mm Hg. As blood enters the systemic capillaries, the blood will lose oxygen and gain carbon dioxide because of the pressure difference of the tissues and blood. In systemic capillaries, **P O₂** = 100 mm Hg, but in the tissue cells, **P O₂** = 40 mm Hg. This pressure gradient drives the diffusion of oxygen out of the capillaries and into the tissue cells. At the same time, blood **P CO₂** = 40 mm Hg and systemic tissue **P CO₂** = 45 mm Hg. The pressure gradient drives CO₂ out of tissue cells and into the capillaries. The blood returning to the lungs through the pulmonary arteries has a venous **P O₂** = 40 mm Hg and a **P CO₂** = 45 mm Hg. The blood enters the lung capillaries where the process of exchanging gases between the capillaries and alveoli begins again ([\[link\]](#)).

Visual Connection

The partial pressures of oxygen and carbon dioxide change as blood moves through the body.



Which of the following statements is false?

1. In the tissues, $P O_2$ drops as blood passes from the arteries to the veins, while $P CO_2$ increases.
2. Blood travels from the lungs to the heart to body tissues, then back to the heart, then the lungs.
3. Blood travels from the lungs to the heart to body tissues, then back to the lungs, then the heart.
4. $P O_2$ is higher in air than in the lungs.

In short, the change in partial pressure from the alveoli to the capillaries drives the oxygen into the tissues and the carbon dioxide into the blood from the tissues. The blood is then transported to the lungs where differences in pressure in the alveoli

result in the movement of carbon dioxide out of the blood into the lungs, and oxygen into the blood.

Link to Learning

Watch this video to learn how to carry out spirometry.

<https://www.openstax.org/l/spirometry>

Section Summary

The lungs can hold a large volume of air, but they are not usually filled to maximal capacity. Lung volume measurements include tidal volume, expiratory reserve volume, inspiratory reserve volume, and residual volume. The sum of these equals the total lung capacity. Gas movement into or out of the lungs is dependent on the pressure of the gas. Air is a mixture of gases; therefore, the partial pressure of each gas can be calculated to determine how the gas will flow in the lung. The difference between the partial pressure of the gas in the air drives oxygen into the tissues and carbon dioxide out of the body.

Visual Connection Questions

[link] Which of the following statements is false?

1. In the tissues, P O₂ drops as blood passes from the arteries to the veins, while P CO₂ increases.
2. Blood travels from the lungs to the heart to body tissues, then back to the heart, then the lungs.
3. Blood travels from the lungs to the heart to body tissues, then back to the lungs, then the heart.
4. P O₂ is higher in air than in the lungs.

[link] C

Review Questions

The inspiratory reserve volume measures the _____.

1. amount of air remaining in the lung after a maximal exhalation
2. amount of air that the lung holds

-
- 3. amount of air that can be further exhaled after a normal breath
 - 4. amount of air that can be further inhaled after a normal breath
-

D

Of the following, which does not explain why the partial pressure of oxygen is lower in the lung than in the external air?

- 1. Air in the lung is humidified; therefore, water vapor pressure alters the pressure.
 - 2. Carbon dioxide mixes with oxygen.
 - 3. Oxygen is moved into the blood and is headed to the tissues.
 - 4. Lungs exert a pressure on the air to reduce the oxygen pressure.
-

D

The total lung capacity is calculated using which of the following formulas?

- 1. residual volume + tidal volume + inspiratory reserve volume
- 2. residual volume + expiratory reserve volume + inspiratory reserve volume

3. expiratory reserve volume + tidal volume
+ inspiratory reserve volume
 4. residual volume + expiratory reserve
volume + tidal volume + inspiratory
reserve volume
-

D

Critical Thinking Questions

What does FEV1/FVC measure? What factors may affect FEV1/FVC?

FEV1/FVC measures the forced expiratory volume in one second in relation to the total forced vital capacity (the total amount of air that is exhaled from the lung from a maximal inhalation). This ratio changes with alterations in lung function that arise from diseases such as fibrosis, asthma, and COPD.

What is the reason for having residual volume in the lung?

If all the air in the lung were exhaled, then

opening the alveoli for the next inspiration would be very difficult. This is because the tissues would stick together.

How can a decrease in the percent of oxygen in the air affect the movement of oxygen in the body?

Oxygen moves from the lung to the bloodstream to the tissues according to the pressure gradient. This is measured as the partial pressure of oxygen. If the amount of oxygen drops in the inspired air, there would be reduced partial pressure. This would decrease the driving force that moves the oxygen into the blood and into the tissues. P O₂ is also reduced at high elevations: P O₂ at high elevations is lower than at sea level because the total atmospheric pressure is less than atmospheric pressure at sea level.

If a patient has increased resistance in his or her lungs, how can this be detected by a doctor? What does this mean?

A doctor can detect a restrictive disease using spirometry. By detecting the rate at which air can be expelled from the lung, a diagnosis of

fibrosis or another restrictive disease can be made.

Glossary

alveolar P O 2

partial pressure of oxygen in the alveoli
(usually around 100 mmHg)

expiratory reserve volume (ERV)

amount of additional air that can be exhaled
after a normal exhalation

FEV1/FVC ratio

ratio of how much air can be forced out of the lung in one second to the total amount that is forced out of the lung; a measurement of lung function that can be used to detect disease states

forced expiratory volume (FEV)

(also, forced vital capacity) measure of how much air can be forced out of the lung from maximal inspiration over a specific amount of time

functional residual capacity (FRC)

expiratory reserve volume plus residual volume

inspiratory capacity (IC)

tidal volume plus inspiratory reserve volume

inspiratory reserve volume (IRV)

amount of additional air that can be inspired after a normal inhalation

lung capacity

measurement of two or more lung volumes
(how much air can be inhaled from the end of an expiration to maximal capacity)

lung volume

measurement of air for one lung function
(normal inhalation or exhalation)

partial pressure

amount of pressure exerted by one gas within a mixture of gases

residual volume (RV)

amount of air remaining in the lung after a maximal expiration

respiratory quotient (RQ)

ratio of carbon dioxide production to each oxygen molecule consumed

spirometry

method to measure lung volumes and to diagnose lung diseases

tidal volume (TV)

amount of air that is inspired and expired

during normal breathing

total lung capacity (TLC)

sum of the residual volume, expiratory reserve volume, tidal volume, and inspiratory reserve volume

venous P CO₂

partial pressure of carbon dioxide in the veins
(40 mm Hg in the pulmonary veins)

venous P O₂

partial pressure of oxygen in the veins (100 mm Hg in the pulmonary veins)

vital capacity (VC)

sum of the expiratory reserve volume, tidal volume, and inspiratory reserve volume

Breathing

By the end of this section, you will be able to:

- Describe how the structures of the lungs and thoracic cavity control the mechanics of breathing
- Explain the importance of compliance and resistance in the lungs
- Discuss problems that may arise due to a V/Q mismatch

Mammalian lungs are located in the thoracic cavity where they are surrounded and protected by the rib cage, intercostal muscles, and bound by the chest wall. The bottom of the lungs is contained by the diaphragm, a skeletal muscle that facilitates breathing. Breathing requires the coordination of the lungs, the chest wall, and most importantly, the diaphragm.

Types of Breathing

Amphibians have evolved multiple ways of breathing. Young amphibians, like tadpoles, use gills to breathe, and they don't leave the water. Some amphibians retain gills for life. As the tadpole grows, the gills disappear and lungs grow. These lungs are primitive and not as evolved as mammalian lungs. Adult amphibians are lacking or

have a reduced diaphragm, so breathing via lungs is forced. The other means of breathing for amphibians is diffusion across the skin. To aid this diffusion, amphibian skin must remain moist.

Birds face a unique challenge with respect to breathing: They fly. Flying consumes a great amount of energy; therefore, birds require a lot of oxygen to aid their metabolic processes. Birds have evolved a respiratory system that supplies them with the oxygen needed to enable flying. Similar to mammals, birds have lungs, which are organs specialized for gas exchange. Oxygenated air, taken in during inhalation, diffuses across the surface of the lungs into the bloodstream, and carbon dioxide diffuses from the blood into the lungs and expelled during exhalation. The details of breathing between birds and mammals differ substantially.

In addition to lungs, birds have air sacs inside their body. Air flows in one direction from the posterior air sacs to the lungs and out of the anterior air sacs. The flow of air is in the opposite direction from blood flow, and gas exchange takes place much more efficiently. This type of breathing enables birds to obtain the requisite oxygen, even at higher altitudes where the oxygen concentration is low. This directionality of airflow requires two cycles of air intake and exhalation to completely get the air out of the lungs.

Evolution Connection

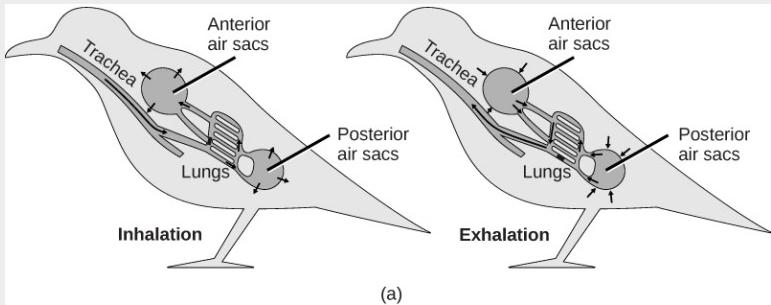
Avian Respiration

Birds have evolved a respiratory system that enables them to fly. Flying is a high-energy process and requires a lot of oxygen. Furthermore, many birds fly in high altitudes where the concentration of oxygen is low. How did birds evolve a respiratory system that is so unique?

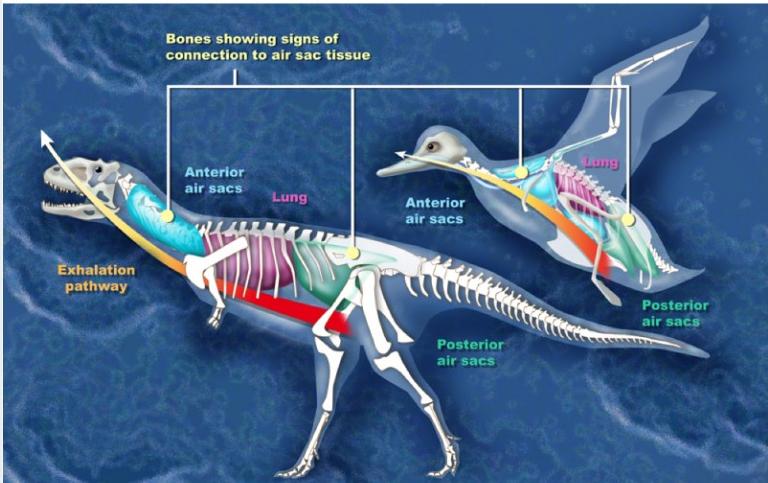
Decades of research by paleontologists have shown that birds evolved from theropods, meat-eating dinosaurs ([\[link\]](#)). In fact, fossil evidence shows that meat-eating dinosaurs that lived more than 100 million years ago had a similar flow-through respiratory system with lungs and air sacs.

Archaeopteryx and *Xiaotingia*, for example, were flying dinosaurs and are believed to be early precursors of birds.

- (a) Birds have a flow-through respiratory system in which air flows unidirectionally from the posterior sacs into the lungs, then into the anterior air sacs. The air sacs connect to openings in hollow bones.
- (b) Dinosaurs, from which birds descended, have similar hollow bones and are believed to have had a similar respiratory system. (credit b: modification of work by Zina Deretsky, National Science Foundation)



(a)



(b)

Most of us consider that dinosaurs are extinct. However, modern birds are descendants of avian dinosaurs. The respiratory system of modern birds has been evolving for hundreds of millions of years.

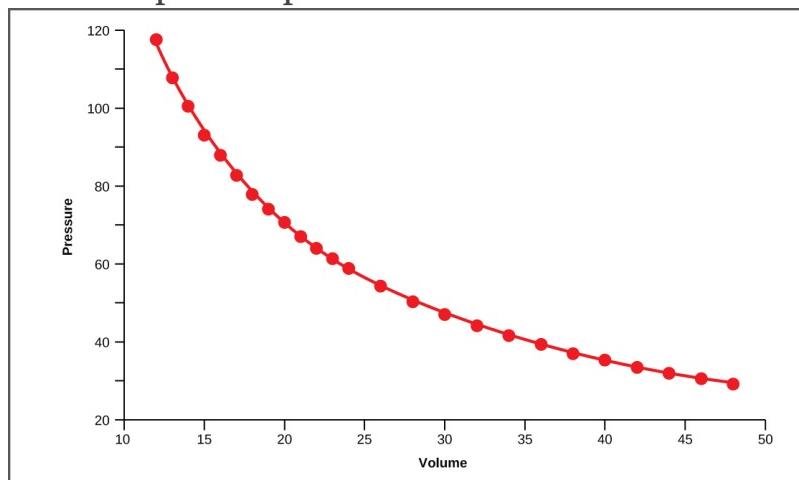
All mammals have lungs that are the main organs for breathing. Lung capacity has evolved to support the animal's activities. During inhalation, the lungs expand with air, and oxygen diffuses across the

lung's surface and enters the bloodstream. During exhalation, the lungs expel air and lung volume decreases. In the next few sections, the process of human breathing will be explained.

This graph shows data from Boyle's original 1662 experiment, which shows that pressure and volume are inversely related. No units are given as Boyle used arbitrary units in his experiments. The lungs, chest wall, and diaphragm are all involved in respiration, both (a) inhalation and (b) expiration. (credit: modification of work by Mariana Ruiz Villareal)

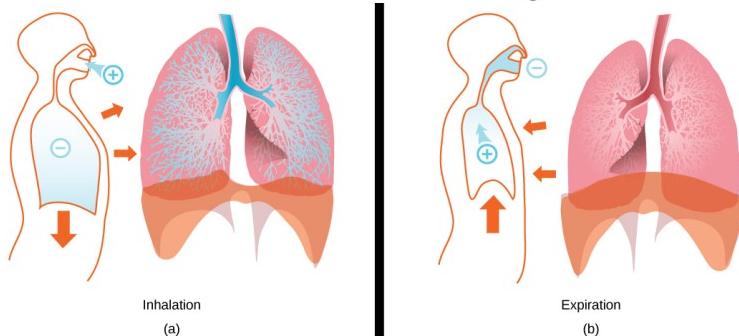
The Mechanics of Human Breathing

Boyle's Law is the gas law that states that in a closed space, pressure and volume are inversely related. As volume decreases, pressure increases and vice versa ([\[link\]](#)). The relationship between gas pressure and volume helps to explain the mechanics of breathing.



There is always a slightly negative pressure within the thoracic cavity, which aids in keeping the airways of the lungs open. During inhalation, volume increases as a result of contraction of the diaphragm, and pressure decreases (according to Boyle's Law). This decrease of pressure in the thoracic cavity relative to the environment makes the cavity less than the atmosphere ([\[link\]](#)a).

Because of this drop in pressure, air rushes into the respiratory passages. To increase the volume of the lungs, the chest wall expands. This results from the contraction of the **intercostal muscles**, the muscles that are connected to the rib cage. Lung volume expands because the diaphragm contracts and the intercostals muscles contract, thus expanding the thoracic cavity. This increase in the volume of the thoracic cavity lowers pressure compared to the atmosphere, so air rushes into the lungs, thus increasing its volume. The resulting increase in volume is largely attributed to an increase in alveolar space, because the bronchioles and bronchi are stiff structures that do not change in size.



The chest wall expands out and away from the

lungs. The lungs are elastic; therefore, when air fills the lungs, the **elastic recoil** within the tissues of the lung exerts pressure back toward the interior of the lungs. These outward and inward forces compete to inflate and deflate the lung with every breath. Upon exhalation, the lungs recoil to force the air out of the lungs, and the intercostal muscles relax, returning the chest wall back to its original position ([\[link\]b](#)). The diaphragm also relaxes and moves higher into the thoracic cavity. This increases the pressure within the thoracic cavity relative to the environment, and air rushes out of the lungs. The movement of air out of the lungs is a passive event. No muscles are contracting to expel the air.

Link to Learning



View how Boyle's Law is related to breathing and watch a [video](#) on Boyle's Law.

https://www.openstaxcollege.org/l/boyle_breathing

The ratio of FEV1 (the amount of air that can be forcibly exhaled in one second after taking a deep breath) to FVC (the total amount of air that can be forcibly exhaled) can be used to diagnose whether a person has restrictive or obstructive lung disease. In restrictive lung disease, FVC is reduced but airways are not obstructed, so the person is able to expel air reasonably fast. In obstructive lung disease, airway obstruction results in slow exhalation as well as reduced FVC. Thus, the FEV1/FVC ratio is lower in persons with obstructive lung disease (less than 69 percent) than in persons with restrictive disease (88 to 90 percent).

The Work of Breathing

The number of breaths per minute is the **respiratory rate**. On average, under non-exertion conditions, the human respiratory rate is 12–15 breaths/minute. The respiratory rate contributes to the **alveolar ventilation**, or how much air moves into and out of the alveoli. Alveolar ventilation prevents carbon dioxide buildup in the alveoli. There are two ways to keep the alveolar ventilation constant: increase the respiratory rate while decreasing the tidal volume of air per breath (shallow breathing), or decrease the respiratory rate while increasing the tidal volume per breath. In either case, the ventilation remains the same, but the work done and type of work needed are quite different. Both tidal volume and respiratory rate are

closely regulated when oxygen demand increases.

There are two types of work conducted during respiration, flow-resistive and elastic work. **Flow-resistive** refers to the work of the alveoli and tissues in the lung, whereas **elastic work** refers to the work of the intercostal muscles, chest wall, and diaphragm. Increasing the respiration rate increases the flow-resistive work of the airways and decreases the elastic work of the muscles. Decreasing the respiratory rate reverses the type of work required.

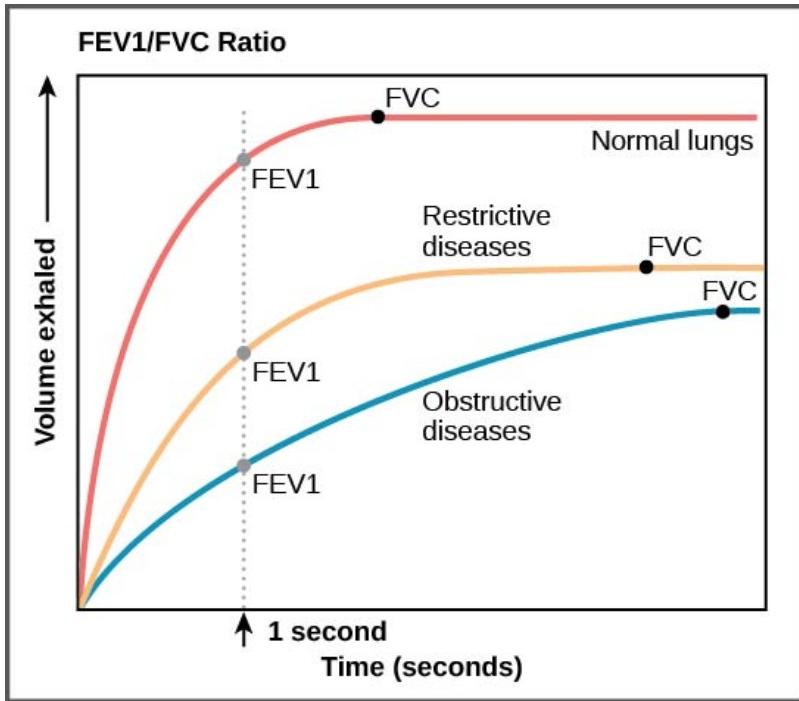
Lung Resistance and Compliance

Pulmonary diseases reduce the rate of gas exchange into and out of the lungs. Two main causes of decreased gas exchange are **compliance** (how elastic the lung is) and **resistance** (how much obstruction exists in the airways). A change in either can dramatically alter breathing and the ability to take in oxygen and release carbon dioxide.

Examples of **restrictive diseases** are respiratory distress syndrome and pulmonary fibrosis. In both diseases, the airways are less compliant and they are stiff or fibrotic. There is a decrease in compliance because the lung tissue cannot bend and move. In these types of restrictive diseases, the intrapleural pressure is more positive and the airways collapse upon exhalation, which traps air in the lungs. **Forced or functional vital capacity (FVC)**, which is

the amount of air that can be forcibly exhaled after taking the deepest breath possible, is much lower than in normal patients, and the time it takes to exhale most of the air is greatly prolonged ([\[link\]](#)). A patient suffering from these diseases cannot exhale the normal amount of air.

Obstructive diseases and conditions include emphysema, asthma, and pulmonary edema. In emphysema, which mostly arises from smoking tobacco, the walls of the alveoli are destroyed, decreasing the surface area for gas exchange. The overall compliance of the lungs is increased, because as the alveolar walls are damaged, lung elastic recoil decreases due to a loss of elastic fibers, and more air is trapped in the lungs at the end of exhalation. Asthma is a disease in which inflammation is triggered by environmental factors. Inflammation obstructs the airways. The obstruction may be due to edema (fluid accumulation), smooth muscle spasms in the walls of the bronchioles, increased mucus secretion, damage to the epithelia of the airways, or a combination of these events. Those with asthma or edema experience increased occlusion from increased inflammation of the airways. This tends to block the airways, preventing the proper movement of gases ([\[link\]](#)). Those with obstructive diseases have large volumes of air trapped after exhalation and breathe at a very high lung volume to compensate for the lack of airway recruitment.



Section Summary

The structure of the lungs and thoracic cavity control the mechanics of breathing. Upon inspiration, the diaphragm contracts and lowers. The intercostal muscles contract and expand the chest wall outward. The intrapleural pressure drops, the lungs expand, and air is drawn into the airways. When exhaling, the intercostal muscles and diaphragm relax, returning the intrapleural pressure back to the resting state. The lungs recoil and airways close. The air passively exits the lung. There is high surface tension at the air-airway interface in

the lung. Surfactant, a mixture of phospholipids and lipoproteins, acts like a detergent in the airways to reduce surface tension and allow for opening of the alveoli.

Breathing and gas exchange are both altered by changes in the compliance and resistance of the lung. If the compliance of the lung decreases, as occurs in restrictive diseases like fibrosis, the airways stiffen and collapse upon exhalation. Air becomes trapped in the lungs, making breathing more difficult. If resistance increases, as happens with asthma or emphysema, the airways become obstructed, trapping air in the lungs and causing breathing to become difficult. Alterations in the ventilation of the airways or perfusion of the arteries can affect gas exchange. These changes in ventilation and perfusion, called V/Q mismatch, can arise from anatomical or physiological changes.

Review Questions

How would paralysis of the diaphragm alter inspiration?

1. It would prevent contraction of the intercostal muscles.
2. It would prevent inhalation because the

- intrapleural pressure would not change.
3. It would decrease the intrapleural pressure and allow more air to enter the lungs.
 4. It would slow expiration because the lung would not relax.
-

B

Restrictive airway diseases _____.

1. increase the compliance of the lung
 2. decrease the compliance of the lung
 3. increase the lung volume
 4. decrease the work of breathing
-

B

Alveolar ventilation remains constant when

_____.

1. the respiratory rate is increased while the volume of air per breath is decreased
 2. the respiratory rate and the volume of air per breath are increased
 3. the respiratory rate is decreased while increasing the volume per breath
 4. both a and c
-

D

Free Response

How would increased airway resistance affect intrapleural pressure during inhalation?

Increased airway resistance increases the volume and pressure in the lung; therefore, the intrapleural pressure would be less negative and breathing would be more difficult.

Explain how a puncture to the thoracic cavity (from a knife wound, for instance) could alter the ability to inhale.

A puncture to the thoracic cavity would equalize the pressure inside the thoracic cavity to the outside environment. For the lung to function properly, the intrapleural pressure must be negative. This is caused by the contraction of the diaphragm pulling the lungs down and drawing air into the lungs.

When someone is standing, gravity stretches the

bottom of the lung down toward the floor to a greater extent than the top of the lung. What implication could this have on the flow of air in the lungs? Where does gas exchange occur in the lungs?

The lung is particularly susceptible to changes in the magnitude and direction of gravitational forces. When someone is standing or sitting upright, the pleural pressure gradient leads to increased ventilation further down in the lung.

Glossary

alveolar ventilation

how much air is in the alveoli

anatomical dead space

(also, anatomical shunt) region of the lung that lacks proper ventilation/perfusion due to an anatomical block

compliance

measurement of the elasticity of the lung

dead space

area in the lung that lacks proper ventilation or perfusion

elastic recoil

property of the lung that drives the lung tissue inward

elastic work

work conducted by the intercostal muscles, chest wall, and diaphragm

flow-resistive

work of breathing performed by the alveoli and tissues in the lung

functional vital capacity (FVC)

amount of air that can be forcibly exhaled after taking the deepest breath possible

intercostal muscle

muscle connected to the rib cage that contracts upon inspiration

intrapleural space

space between the layers of pleura

obstructive disease

disease (such as emphysema and asthma) that arises from obstruction of the airways; compliance increases in these diseases

physiological dead space

(also, physiological shunt) region of the lung that lacks proper ventilation/perfusion due to a physiological change in the lung (like inflammation or edema)

pleura

tissue layer that surrounds the lungs and lines the interior of the thoracic cavity

pleurisy

painful inflammation of the pleural tissue layers

recruitment

process of opening airways that normally remain closed when the cardiac output increases

resistance

measurement of lung obstruction

respiratory distress syndrome

disease that arises from a deficient amount of surfactant

respiratory rate

number of breaths per minute

restrictive disease

disease that results from a restriction and decreased compliance of the alveoli; respiratory distress syndrome and pulmonary fibrosis are examples

surfactant

detergent-like liquid in the airways that lowers the surface tension of the alveoli to

allow for expansion

ventilation/perfusion (V/Q) mismatch

region of the lung that lacks proper alveolar ventilation (V) and/or arterial perfusion (Q)

Transport of Gases in Human Bodily Fluids

By the end of this section, you will be able to:

- Describe how oxygen is bound to hemoglobin and transported to body tissues
- Explain how carbon dioxide is transported from body tissues to the lungs

Once the oxygen diffuses across the alveoli, it enters the bloodstream and is transported to the tissues where it is unloaded, and carbon dioxide diffuses out of the blood and into the alveoli to be expelled from the body. Although gas exchange is a continuous process, the oxygen and carbon dioxide are transported by different mechanisms.

The protein inside (a) red blood cells that carries oxygen to cells and carbon dioxide to the lungs is (b) hemoglobin. Hemoglobin is made up of four symmetrical subunits and four heme groups. Iron associated with the heme binds oxygen. It is the iron in hemoglobin that gives blood its red color. Individuals with sickle cell anemia have crescent-shaped red blood cells. (credit: modification of work by Ed Uthman; scale-bar data from Matt Russell)

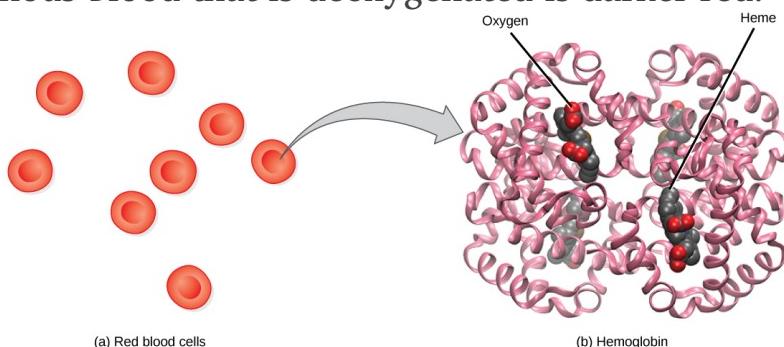
Transport of Oxygen in the Blood

Although oxygen dissolves in blood, only a small amount of oxygen is transported this way. Only 1.5 percent of oxygen in the blood is dissolved directly

into the blood itself. Most oxygen—98.5 percent—is bound to a protein called hemoglobin and carried to the tissues.

Hemoglobin

Hemoglobin, or Hb, is a protein molecule found in red blood cells (erythrocytes) made of four subunits: two alpha subunits and two beta subunits ([\[link\]](#)). Each subunit surrounds a central **heme group** that contains iron and binds one oxygen molecule, allowing each hemoglobin molecule to bind four oxygen molecules. Molecules with more oxygen bound to the heme groups are brighter red. As a result, oxygenated arterial blood where the Hb is carrying four oxygen molecules is bright red, while venous blood that is deoxygenated is darker red.

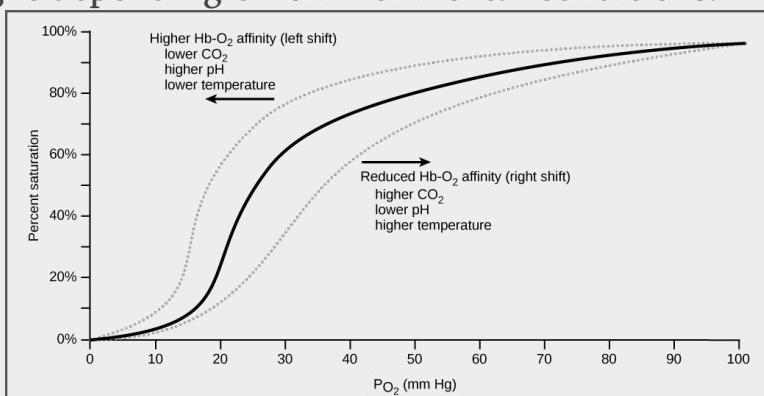


It is easier to bind a second and third oxygen molecule to Hb than the first molecule. This is because the hemoglobin molecule changes its shape, or conformation, as oxygen binds. The fourth oxygen is then more difficult to bind. The binding of

oxygen to hemoglobin can be plotted as a function of the partial pressure of oxygen in the blood (x-axis) versus the relative Hb-oxygen saturation (y-axis). The resulting graph—an **oxygen dissociation curve**—is sigmoidal, or S-shaped ([\[link\]](#)). As the partial pressure of oxygen increases, the hemoglobin becomes increasingly saturated with oxygen.

Art Connection

The oxygen dissociation curve demonstrates that, as the partial pressure of oxygen increases, more oxygen binds hemoglobin. However, the affinity of hemoglobin for oxygen may shift to the left or the right depending on environmental conditions.



The kidneys are responsible for removing excess H^+ ions from the blood. If the kidneys fail, what would happen to blood pH and to hemoglobin affinity for oxygen?

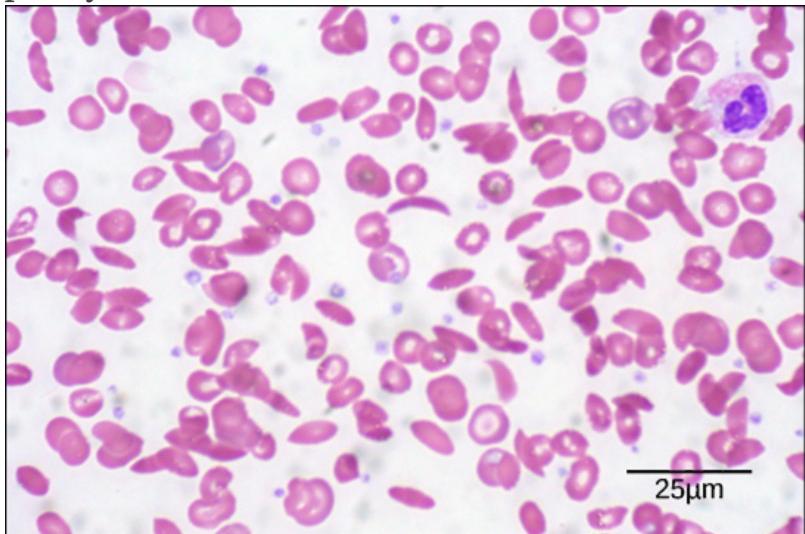
Factors That Affect Oxygen Binding

The **oxygen-carrying capacity** of hemoglobin determines how much oxygen is carried in the blood. In addition to P O_2 , other environmental factors and diseases can affect oxygen carrying capacity and delivery.

Carbon dioxide levels, blood pH, and body temperature affect oxygen-carrying capacity ([\[link\]](#)). When carbon dioxide is in the blood, it reacts with water to form bicarbonate (HCO_3^-) and hydrogen ions (H^+). As the level of carbon dioxide in the blood increases, more H^+ is produced and the pH decreases. This increase in carbon dioxide and subsequent decrease in pH reduce the affinity of hemoglobin for oxygen. The oxygen dissociates from the Hb molecule, shifting the oxygen dissociation curve to the right. Therefore, more oxygen is needed to reach the same hemoglobin saturation level as when the pH was higher. A similar shift in the curve also results from an increase in body temperature. Increased temperature, such as from increased activity of skeletal muscle, causes the affinity of hemoglobin for oxygen to be reduced.

Diseases like sickle cell anemia and thalassemia decrease the blood's ability to deliver oxygen to tissues and its oxygen-carrying capacity. In **sickle cell anemia**, the shape of the red blood cell is

crescent-shaped, elongated, and stiffened, reducing its ability to deliver oxygen ([\[link\]](#)). In this form, red blood cells cannot pass through the capillaries. This is painful when it occurs. **Thalassemia** is a rare genetic disease caused by a defect in either the alpha or the beta subunit of Hb. Patients with thalassemia produce a high number of red blood cells, but these cells have lower-than-normal levels of hemoglobin. Therefore, the oxygen-carrying capacity is diminished.



As percent CO increases, the oxygen saturation of hemoglobin decreases.

Transport of Carbon Dioxide in the Blood

Carbon dioxide molecules are transported in the blood from body tissues to the lungs by one of three methods: dissolution directly into the blood, binding to hemoglobin, or carried as a bicarbonate ion.

Several properties of carbon dioxide in the blood affect its transport. First, carbon dioxide is more soluble in blood than oxygen. About 5 to 7 percent of all carbon dioxide is dissolved in the plasma. Second, carbon dioxide can bind to plasma proteins or can enter red blood cells and bind to hemoglobin. This form transports about 10 percent of the carbon dioxide. When carbon dioxide binds to hemoglobin, a molecule called **carbaminohemoglobin** is formed. Binding of carbon dioxide to hemoglobin is reversible. Therefore, when it reaches the lungs, the carbon dioxide can freely dissociate from the hemoglobin and be expelled from the body.

Third, the majority of carbon dioxide molecules (85 percent) are carried as part of the **bicarbonate buffer system**. In this system, carbon dioxide diffuses into the red blood cells. **Carbonic anhydrase (CA)** within the red blood cells quickly converts the carbon dioxide into carbonic acid (H_2CO_3). Carbonic acid is an unstable intermediate molecule that immediately dissociates into **bicarbonate ions (HCO_3^-)** and hydrogen (H^+) ions. Since carbon dioxide is quickly converted into bicarbonate ions, this reaction allows for the continued uptake of carbon dioxide into the blood down its concentration gradient. It also results in the production of H^+ ions. If too much H^+ is produced, it can alter blood pH. However, hemoglobin binds to the free H^+ ions and thus limits shifts in pH. The newly synthesized

bicarbonate ion is transported out of the red blood cell into the liquid component of the blood in exchange for a chloride ion (Cl^-); this is called the **chloride shift**. When the blood reaches the lungs, the bicarbonate ion is transported back into the red blood cell in exchange for the chloride ion. The H^+ ion dissociates from the hemoglobin and binds to the bicarbonate ion. This produces the carbonic acid intermediate, which is converted back into carbon dioxide through the enzymatic action of CA. The carbon dioxide produced is expelled through the lungs during exhalation.

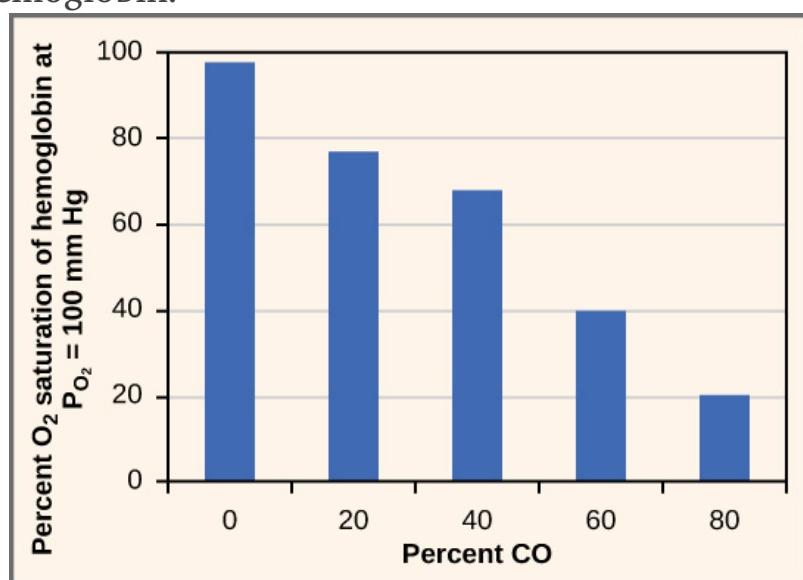


The benefit of the bicarbonate buffer system is that carbon dioxide is “soaked up” into the blood with little change to the pH of the system. This is important because it takes only a small change in the overall pH of the body for severe injury or death to result. The presence of this bicarbonate buffer system also allows for people to travel and live at high altitudes: When the partial pressure of oxygen and carbon dioxide change at high altitudes, the bicarbonate buffer system adjusts to regulate carbon dioxide while maintaining the correct pH in the body.

Carbon Monoxide Poisoning

While carbon dioxide can readily associate and

dissociate from hemoglobin, other molecules such as carbon monoxide (CO) cannot. Carbon monoxide has a greater affinity for hemoglobin than oxygen. Therefore, when carbon monoxide is present, it binds to hemoglobin preferentially over oxygen. As a result, oxygen cannot bind to hemoglobin, so very little oxygen is transported through the body ([\[link\]](#)). Carbon monoxide is a colorless, odorless gas and is therefore difficult to detect. It is produced by gas-powered vehicles and tools. Carbon monoxide can cause headaches, confusion, and nausea; long-term exposure can cause brain damage or death. Administering 100 percent (pure) oxygen is the usual treatment for carbon monoxide poisoning. Administration of pure oxygen speeds up the separation of carbon monoxide from hemoglobin.



Section Summary

Hemoglobin is a protein found in red blood cells that is comprised of two alpha and two beta subunits that surround an iron-containing heme group. Oxygen readily binds this heme group. The ability of oxygen to bind increases as more oxygen molecules are bound to heme. Disease states and altered conditions in the body can affect the binding ability of oxygen, and increase or decrease its ability to dissociate from hemoglobin.

Carbon dioxide can be transported through the blood via three methods. It is dissolved directly in the blood, bound to plasma proteins or hemoglobin, or converted into bicarbonate. The majority of carbon dioxide is transported as part of the bicarbonate system. Carbon dioxide diffuses into red blood cells. Inside, carbonic anhydrase converts carbon dioxide into carbonic acid (H_2CO_3), which is subsequently hydrolyzed into bicarbonate (HCO_3^-) and H^+ . The H^+ ion binds to hemoglobin in red blood cells, and bicarbonate is transported out of the red blood cells in exchange for a chloride ion. This is called the chloride shift. Bicarbonate leaves the red blood cells and enters the blood plasma. In the lungs, bicarbonate is transported back into the red blood cells in exchange for chloride. The H^+ dissociates from hemoglobin and combines with bicarbonate to form carbonic acid with the help of carbonic anhydrase, which further catalyzes the

reaction to convert carbonic acid back into carbon dioxide and water. The carbon dioxide is then expelled from the lungs.

Art Connections

[\[link\]](#) The kidneys are responsible for removing excess H⁺ ions from the blood. If the kidneys fail, what would happen to blood pH and to hemoglobin affinity for oxygen?

[\[link\]](#) The blood pH will drop and hemoglobin affinity for oxygen will decrease.

Review Questions

Which of the following will NOT facilitate the transfer of oxygen to tissues?

1. decreased body temperature
 2. decreased pH of the blood
 3. increased carbon dioxide
 4. increased exercise
-

A

The majority of carbon dioxide in the blood is transported by _____.

1. binding to hemoglobin
 2. dissolution in the blood
 3. conversion to bicarbonate
 4. binding to plasma proteins
-

C

The majority of oxygen in the blood is transported by _____.

1. dissolution in the blood
 2. being carried as bicarbonate ions
 3. binding to blood plasma
 4. binding to hemoglobin
-

D

Free Response

What would happen if no carbonic anhydrase

were present in red blood cells?

Without carbonic anhydrase, carbon dioxide would not be hydrolyzed into carbonic acid or bicarbonate. Therefore, very little carbon dioxide (only 15 percent) would be transported in the blood away from the tissues.

How does the administration of 100 percent oxygen save a patient from carbon monoxide poisoning? Why wouldn't giving carbon dioxide work?

Carbon monoxide has a higher affinity for hemoglobin than oxygen. This means that carbon monoxide will preferentially bind to hemoglobin over oxygen. Administration of 100 percent oxygen is an effective therapy because at that concentration, oxygen will displace the carbon monoxide from the hemoglobin.

Glossary

bicarbonate buffer system
system in the blood that absorbs carbon dioxide and regulates pH levels

bicarbonate (HCO_3^-) ion

ion created when carbonic acid dissociates into H⁺ and (HCO₃⁻)

carbaminohemoglobin

molecule that forms when carbon dioxide binds to hemoglobin

carbonic anhydrase (CA)

enzyme that catalyzes carbon dioxide and water into carbonic acid

chloride shift

chloride shift exchange of chloride for bicarbonate into or out of the red blood cell

heme group

centralized iron-containing group that is surrounded by the alpha and beta subunits of hemoglobin

hemoglobin

molecule in red blood cells that can bind oxygen, carbon dioxide, and carbon monoxide

oxygen-carrying capacity

amount of oxygen that can be transported in the blood

oxygen dissociation curve

curve depicting the affinity of oxygen for hemoglobin

sickle cell anemia

genetic disorder that affects the shape of red blood cells, and their ability to transport oxygen and move through capillaries

thalassemia

rare genetic disorder that results in mutation of the alpha or beta subunits of hemoglobin, creating smaller red blood cells with less hemoglobin

Innate Immune Response

By the end of this section, you will be able to do the following:

- Describe physical and chemical immune barriers
- Explain immediate and induced innate immune responses
- Discuss natural killer cells
- Describe major histocompatibility class I molecules
- Summarize how the proteins in a complement system function to destroy extracellular pathogens

The immune system comprises both innate and adaptive immune responses. **Innate immunity** occurs naturally because of genetic factors or physiology; it is not induced by infection or vaccination but works to reduce the workload for the adaptive immune response. Both the innate and adaptive levels of the immune response involve secreted proteins, receptor-mediated signaling, and intricate cell-to-cell communication. The innate immune system developed early in animal evolution, roughly a billion years ago, as an essential response to infection. Innate immunity has a limited number of specific targets: any pathogenic threat triggers a consistent sequence of events that can identify the type of pathogen and either clear the infection independently or mobilize a highly

specialized adaptive immune response. For example, tears and mucus secretions contain microbicidal factors.

Physical and Chemical Barriers

Before any immune factors are triggered, the skin functions as a continuous, impassable barrier to potentially infectious pathogens. Pathogens are killed or inactivated on the skin by desiccation (drying out) and by the skin's acidity. In addition, beneficial microorganisms that coexist on the skin compete with invading pathogens, preventing infection. Regions of the body that are not protected by skin (such as the eyes and mucus membranes) have alternative methods of defense, such as tears and mucus secretions that trap and rinse away pathogens, and cilia in the nasal passages and respiratory tract that push the mucus with the pathogens out of the body. Throughout the body are other defenses, such as the low pH of the stomach (which inhibits the growth of pathogens), blood proteins that bind and disrupt bacterial cell membranes, and the process of urination (which flushes pathogens from the urinary tract).

Despite these barriers, pathogens may enter the body through skin abrasions or punctures, or by collecting on mucosal surfaces in large numbers that overcome the mucus or cilia. Some pathogens have

evolved specific mechanisms that allow them to overcome physical and chemical barriers. When pathogens do enter the body, the innate immune system responds with inflammation, pathogen engulfment, and secretion of immune factors and proteins.

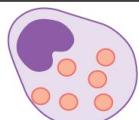
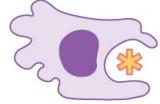
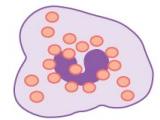
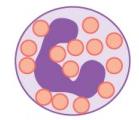
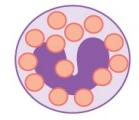
The characteristics and location of cells involved in the innate immune system are described. (credit: modification of work by NIH) Cells of the blood include (1) monocytes, (2) lymphocytes, (3) neutrophils, (4) red blood cells, and (5) platelets. Note the very similar morphologies of the leukocytes (1, 2, 3). (credit: modification of work by Bruce Wetzel, Harry Schaefer, NCI; scale-bar data from Matt Russell) Interferons are cytokines that are released by a cell infected with a virus. Response of neighboring cells to interferon helps stem the infection. In response to a cut, mast cells secrete histamines that cause nearby capillaries to dilate. Neutrophils and monocytes leave the capillaries. Monocytes mature into macrophages. Neutrophils, dendritic cells, and macrophages release chemicals to stimulate the inflammatory response. Neutrophils and macrophages also consume invading bacteria by phagocytosis.

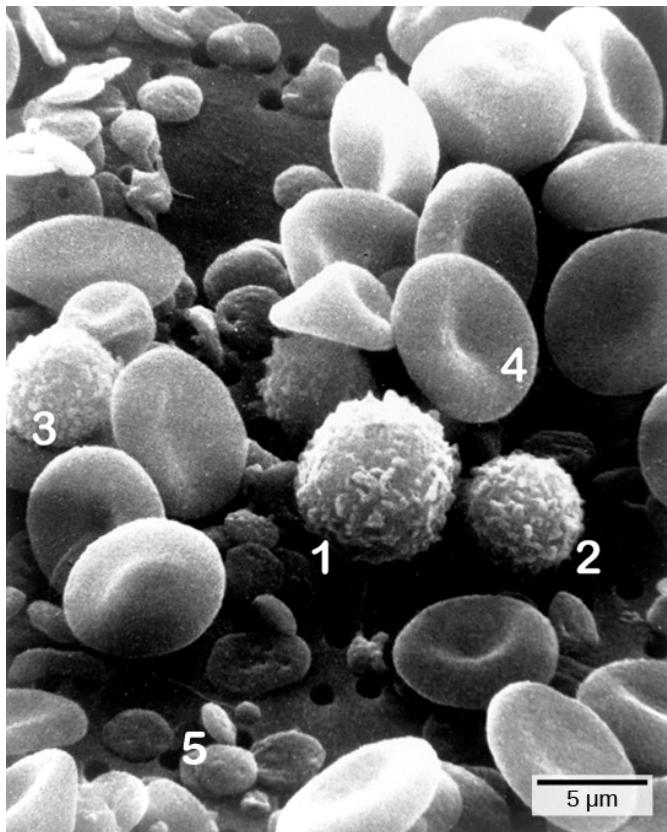
Pathogen Recognition

An infection may be intracellular or extracellular, depending on the pathogen. All viruses infect cells and replicate within those cells (intracellularly),

whereas bacteria and other parasites may replicate intracellularly or extracellularly, depending on the species. The innate immune system must respond accordingly: by identifying the extracellular pathogen and/or by identifying host cells that have already been infected. When a pathogen enters the body, cells in the blood and lymph detect the specific **pathogen-associated molecular patterns (PAMPs)** on the pathogen's surface. PAMPs are carbohydrate, polypeptide, and nucleic acid "signatures" that are expressed by viruses, bacteria, and parasites but which differ from molecules on host cells. The immune system has specific cells, described in [\[link\]](#) and shown in [\[link\]](#), with receptors that recognize these PAMPs. A **macrophage** is a large phagocytic cell that engulfs foreign particles and pathogens. Macrophages recognize PAMPs via complementary **pattern recognition receptors (PRRs)**. PRRs are molecules on macrophages and dendritic cells which are in contact with the external environment. A **monocyte** is a type of white blood cell that circulates in the blood and lymph and differentiates into macrophages after it moves into infected tissue. Dendritic cells bind molecular signatures of pathogens and promote pathogen engulfment and destruction. Toll-like receptors (TLRs) are a type of PRR that recognizes molecules that are shared by pathogens but distinguishable from host molecules. TLRs are present in invertebrates as well as vertebrates, and appear to be one of the most

ancient components of the immune system. TLRs have also been identified in the mammalian nervous system.

Cell type	Characteristics	Location	Image
Mast cell	Dilates blood vessels and induces inflammation through release of histamines and heparin. Recruits macrophages and neutrophils. Involved in wound healing and defense against pathogens but can also be responsible for allergic reactions.	Connective tissues, mucous membranes	 A purple oval-shaped cell with several orange circular organelles inside.
Macrophage	Phagocytic cell that consumes foreign pathogens and cancer cells. Stimulates response of other immune cells.	Migrates from blood vessels into tissues.	 A purple cell with irregular, finger-like projections and a central nucleus, with a small yellow starburst icon nearby.
Natural killer cell	Kills tumor cells and virus-infected cells.	Circulates in blood and migrates into tissues.	 A purple oval cell containing many orange circular objects, some of which appear to be being engulfed or destroyed.
Dendritic cell	Presents antigens on its surface, thereby triggering adaptive immunity.	Present in epithelial tissue, including skin, lung and tissues of the digestive tract. Migrates to lymph nodes upon activation.	 A purple flower-like cell with multiple long, thin processes extending from a central body, with a small yellow starburst icon.
Monocyte	Differentiates into macrophages and dendritic cells in response to inflammation.	Stored in spleen, moves through blood vessels to infected tissues.	 A large, irregularly shaped purple cell with a prominent central nucleus.
Neutrophil	First responders at the site of infection or trauma, this abundant phagocytic cell represents 50-60 percent of all leukocytes. Releases toxins that kill or inhibit bacteria and fungi and recruits other immune cells to the site of infection.	Migrates from blood vessels into tissues.	 A purple cell with a segmented nucleus and many orange circular organelles.
Basophil	Responsible for defense against parasites. Releases histamines that cause inflammation and may be responsible for allergic reactions.	Circulates in blood and migrates to tissues.	 A purple cell with a segmented nucleus and many orange circular organelles.
Eosinophil	Releases toxins that kill bacteria and parasites but also causes tissue damage.	Circulates in blood and migrates to tissues.	 A purple cell with a segmented nucleus and many orange circular organelles.



Cytokine Release Effect

The binding of PRRs with PAMPs triggers the release of cytokines, which signal that a pathogen is present and needs to be destroyed along with any infected cells. A **cytokine** is a chemical messenger that regulates cell differentiation (form and function), proliferation (production), and gene expression to affect immune responses. At least 40 types of cytokines exist in humans that differ in terms of the cell type that produces them, the cell

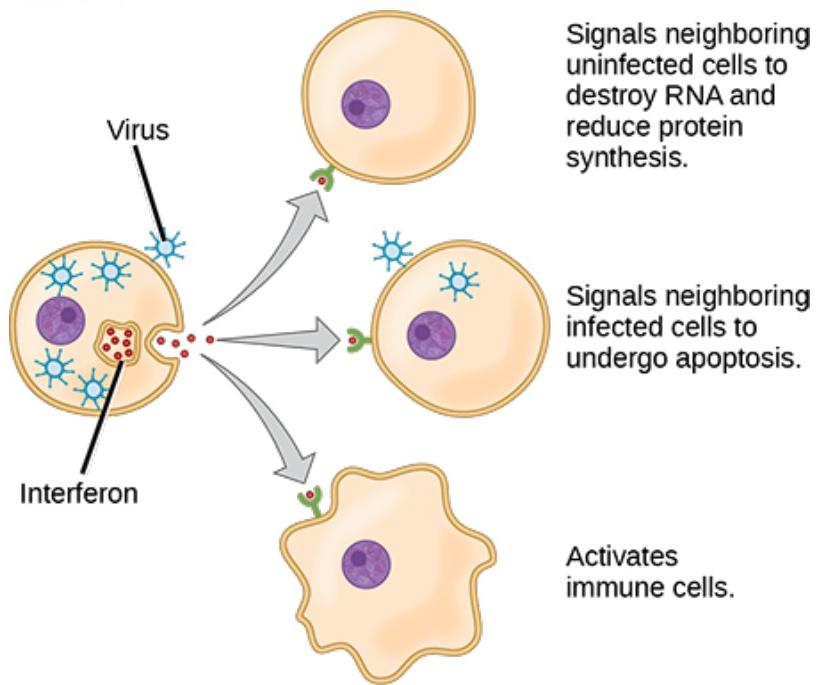
type that responds to them, and the changes they produce. One type of cytokine, interferon, is illustrated in [\[link\]](#).

One subclass of cytokines is the interleukin (IL), so named because they mediate interactions between leukocytes (white blood cells). Interleukins are involved in bridging the innate and adaptive immune responses. In addition to being released from cells after PAMP recognition, cytokines are released by the infected cells which bind to nearby uninfected cells and induce those cells to release cytokines, which results in a cytokine burst.

A second class of early-acting cytokines is interferons, which are released by infected cells as a warning to nearby uninfected cells. One of the functions of an **interferon** is to inhibit viral replication. They also have other important functions, such as tumor surveillance. Interferons work by signaling neighboring uninfected cells to destroy RNA and reduce protein synthesis, signaling neighboring infected cells to undergo apoptosis (programmed cell death), and activating immune cells.

In response to interferons, uninfected cells alter their gene expression, which increases the cells' resistance to infection. One effect of interferon-induced gene expression is a sharply reduced cellular protein synthesis. Virally infected cells

produce more viruses by synthesizing large quantities of viral proteins. Thus, by reducing protein synthesis, a cell becomes resistant to viral infection.

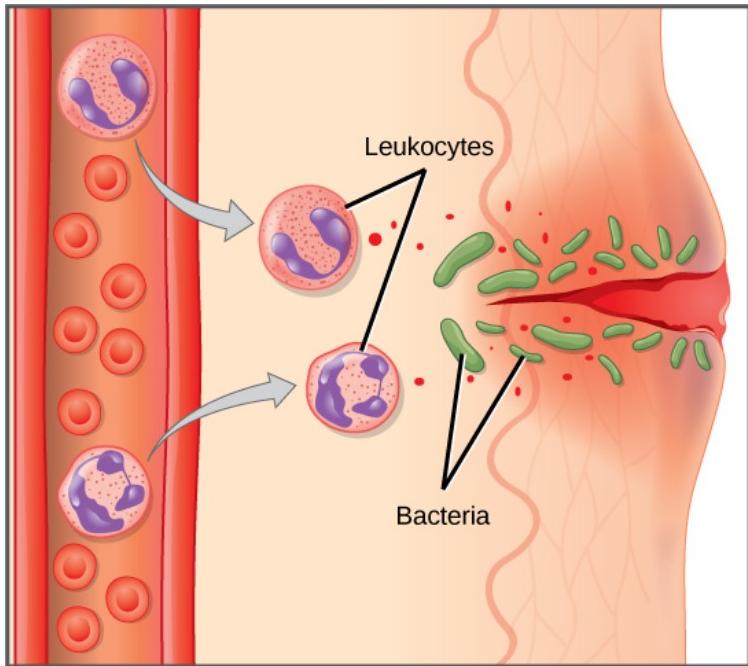


Phagocytosis and Inflammation

The first cytokines to be produced are pro-inflammatory; that is, they encourage **inflammation**, the localized redness, swelling, heat, and pain that result from the movement of leukocytes and fluid through increasingly permeable capillaries to a site of infection. The population of leukocytes that arrives at an infection site depends on the nature of the infecting pathogen. Both macrophages and dendritic cells engulf pathogens

and cellular debris through phagocytosis. A **neutrophil** is also a phagocytic leukocyte that engulfs and digests pathogens. Neutrophils, shown in [\[link\]](#), are the most abundant leukocytes of the immune system. Neutrophils have a nucleus with two to five lobes, and they contain organelles, called lysosomes, that digest engulfed pathogens. An **eosinophil** is a leukocyte that works with other eosinophils to surround a parasite; it is involved in the allergic response and in protection against helminthes (parasitic worms).

Neutrophils and eosinophils are particularly important leukocytes that engulf large pathogens, such as bacteria and fungi. A **mast cell** is a leukocyte that produces inflammatory molecules, such as histamine, in response to large pathogens. A **basophil** is a leukocyte that, like a neutrophil, releases chemicals to stimulate the inflammatory response as illustrated in [\[link\]](#). Basophils are also involved in allergy and hypersensitivity responses and induce specific types of inflammatory responses. Eosinophils and basophils produce additional inflammatory mediators to recruit more leukocytes. A hypersensitive immune response to harmless antigens, such as in pollen, often involves the release of histamine by basophils and mast cells.



Cytokines also send feedback to cells of the nervous system to bring about the overall symptoms of feeling sick, which include lethargy, muscle pain, and nausea. These effects may have evolved because the symptoms encourage the individual to rest and prevent the spreading of the infection to others. Cytokines also increase the core body temperature, causing a fever, which causes the liver to withhold iron from the blood. Without iron, certain pathogens, such as some bacteria, are unable to replicate; this is called nutritional immunity.

Link to Learning

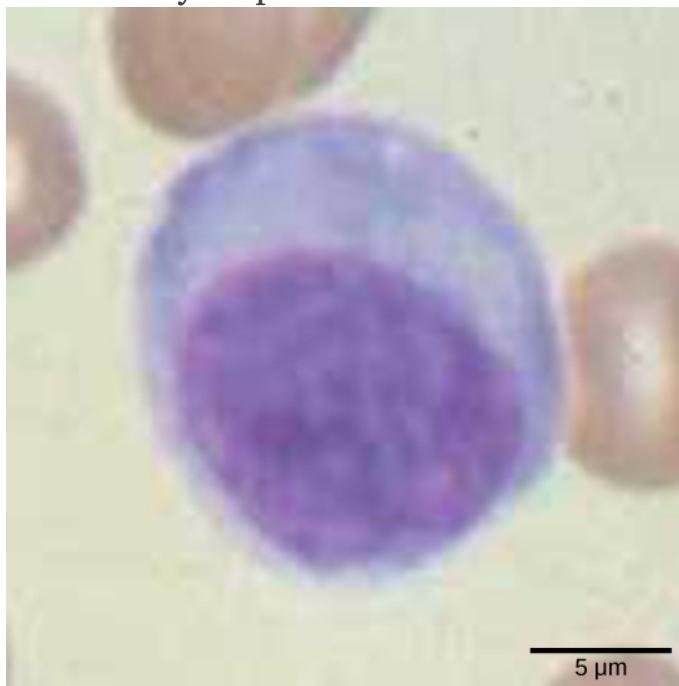
Watch this 23-second stop-motion [video](#) showing a neutrophil that searches for and engulfs fungus spores during an elapsed time of about 79 minutes.

Lymphocytes, such as NK cells, are characterized by their large nuclei that actively absorb Wright stain and therefore appear dark colored under a microscope.

Natural Killer Cells

Lymphocytes are leukocytes that are histologically identifiable by their large, darkly staining nuclei; they are small cells with very little cytoplasm, as shown in [\[link\]](#). Infected cells are identified and destroyed by **natural killer (NK) cells**, lymphocytes that can kill cells infected with viruses or tumor cells (abnormal cells that uncontrollably divide and invade other tissue). T cells and B cells of the adaptive immune system also are classified as lymphocytes. **T cells** are lymphocytes that mature in the thymus gland, and **B cells** are lymphocytes that mature in the bone marrow. NK cells identify intracellular infections, especially from viruses, by the altered expression of **major histocompatibility class (MHC) I molecules** on the surface of infected cells. MHC I molecules are proteins on the surfaces of all nucleated cells, thus they are scarce on red blood cells and platelets which are non-nucleated.

The function of MHC I molecules is to display fragments of proteins from the infectious agents within the cell to T cells; healthy cells will be ignored, while “non-self” or foreign proteins will be attacked by the immune system. MHC II molecules are found mainly on cells containing antigens (“non-self proteins”) and on lymphocytes. **MHC II molecules** interact with helper T cells to trigger the appropriate immune response, which may include the inflammatory response.



An infected cell (or a tumor cell) is usually incapable of synthesizing and displaying MHC I molecules appropriately. The metabolic resources of cells infected by some viruses produce proteins that interfere with MHC I processing and/or trafficking

to the cell surface. The reduced MHC I on host cells varies from virus to virus and results from active inhibitors being produced by the viruses. This process can deplete host MHC I molecules on the cell surface, which NK cells detect as “unhealthy” or “abnormal” while searching for cellular MHC I molecules. Similarly, the dramatically altered gene expression of tumor cells leads to expression of extremely deformed or absent MHC I molecules that also signal “unhealthy” or “abnormal.”

NK cells are always active; an interaction with normal, intact MHC I molecules on a healthy cell disables the killing sequence, and the NK cell moves on. After the NK cell detects an infected or tumor cell, its cytoplasm secretes granules comprised of **perforin**, a destructive protein that creates a pore in the target cell. Granzymes are released along with the perforin in the immunological synapse. A **granzyme** is a protease that digests cellular proteins and induces the target cell to undergo programmed cell death, or apoptosis. Phagocytic cells then digest the cell debris left behind. NK cells are constantly patrolling the body and are an effective mechanism for controlling potential infections and preventing cancer progression.

The classic pathway for the complement cascade involves the attachment of several initial complement proteins to an antibody-bound pathogen followed by rapid activation and binding of many more complement proteins and the creation

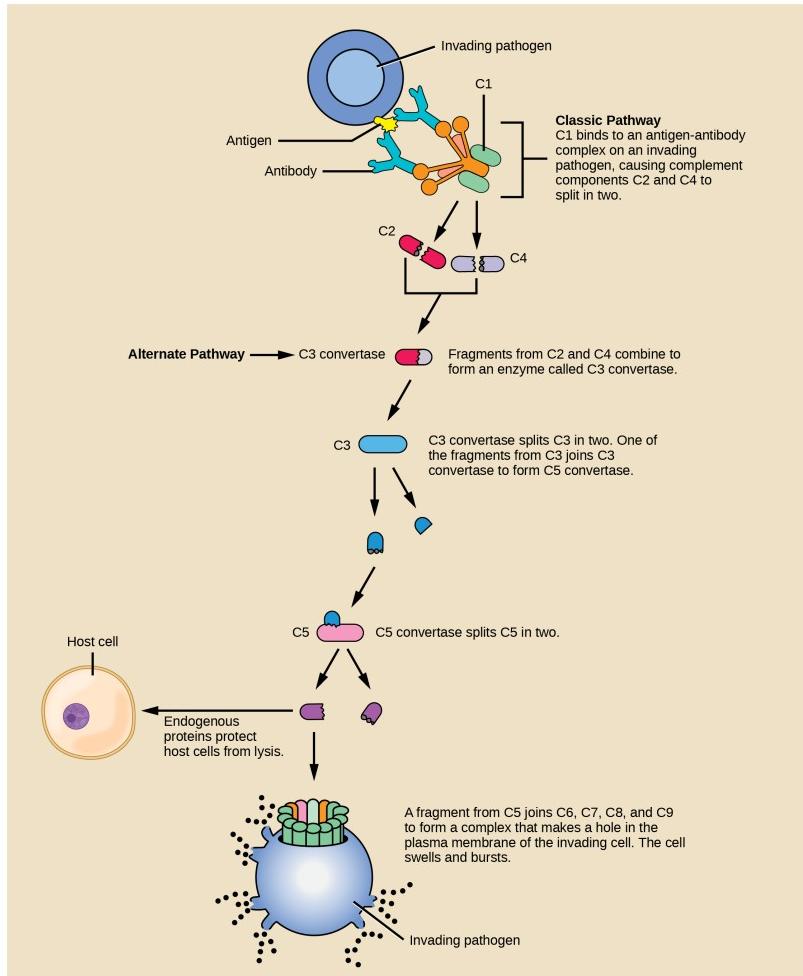
of destructive pores in the microbial cell envelope and cell wall. The alternate pathway does not involve antibody activation. Rather, C3 convertase spontaneously breaks down C3. Endogenous regulatory proteins prevent the complement complex from binding to host cells. Pathogens lacking these regulatory proteins are lysed. (credit: modification of work by NIH)

Complement

An array of approximately 20 types of soluble proteins, called a **complement system**, functions to destroy extracellular pathogens. Cells of the liver and macrophages synthesize complement proteins continuously; these proteins are abundant in the blood serum and are capable of responding immediately to infecting microorganisms. The complement system is so named because it is complementary to the antibody response of the adaptive immune system. Complement proteins bind to the surfaces of microorganisms and are particularly attracted to pathogens that are already bound by antibodies. Binding of complement proteins occurs in a specific and highly regulated sequence, with each successive protein being activated by cleavage and/or structural changes induced upon binding of the preceding protein(s). After the first few complement proteins bind, a cascade of sequential binding events follows in which the pathogen rapidly becomes coated in

complement proteins.

Complement proteins perform several functions. The proteins serve as a marker to indicate the presence of a pathogen to phagocytic cells, such as macrophages and B cells, and enhance engulfment; this process is called **opsonization**. Certain complement proteins can combine to form attack complexes that open pores in microbial cell membranes. These structures destroy pathogens by causing their contents to leak, as illustrated in [\[link\]](#).



Section Summary

The innate immune system serves as a first responder to pathogenic threats that bypass natural physical and chemical barriers of the body. Using a combination of cellular and molecular attacks, the innate immune system identifies the nature of a

pathogen and responds with inflammation, phagocytosis, cytokine release, destruction by NK cells, and/or a complement system. When innate mechanisms are insufficient to clear an infection, the adaptive immune response is informed and mobilized.

Review Questions

Which of the following is a barrier against pathogens provided by the skin?

1. high pH
 2. mucus
 3. tears
 4. desiccation
-

D

Although interferons have several effects, they are particularly useful against infections with which type of pathogen?

1. bacteria
2. viruses
3. fungi
4. helminths

B

Which organelle do phagocytes use to digest engulfed particles?

1. lysosome
 2. nucleus
 3. endoplasmic reticulum
 4. mitochondria
-

A

Which innate immune system component uses MHC I molecules directly in its defense strategy?

1. macrophages
 2. neutrophils
 3. NK cells
 4. interferon
-

C

Critical Thinking Questions

Different MHC I molecules between donor and recipient cells can lead to rejection of a transplanted organ or tissue. Suggest a reason for this.

If the MHC I molecules expressed on donor cells differ from the MHC I molecules expressed on recipient cells, NK cells may identify the donor cells as “non-self” and produce perforin and granzymes to induce the donor cells to undergo apoptosis, which would destroy the transplanted organ.

If a series of genetic mutations prevented some, but not all, of the complement proteins from binding antibodies or pathogens, would the entire complement system be compromised?

The entire complement system would probably be affected even when only a few members were mutated such that they could no longer bind. Because the complement involves the binding of activated proteins in a specific sequence, when one or more proteins in the sequence are absent, the subsequent proteins would be incapable of binding to elicit the complement’s pathogen-destructive effects.

Glossary

basophil

leukocyte that releases chemicals usually involved in the inflammatory response

B cell

lymphocyte that matures in the bone marrow and differentiates into antibody-secreting plasma cells

complement system

array of approximately 20 soluble proteins of the innate immune system that enhance phagocytosis, bore holes in pathogens, and recruit lymphocytes; enhances the adaptive response when antibodies are produced

cytokine

chemical messenger that regulates cell differentiation, proliferation, gene expression, and cell trafficking to effect immune responses

eosinophil

leukocyte that responds to parasites and is involved in the allergic response

granzyme

protease that enters target cells through perforin and induces apoptosis in the target cells; used by NK cells and killer T cells

inflammation

localized redness, swelling, heat, and pain that results from the movement of leukocytes and fluid through opened capillaries to a site of infection

innate immunity

immunity that occurs naturally because of genetic factors or physiology, and is not induced by infection or vaccination

interferon

cytokine that inhibits viral replication and modulates the immune response

lymphocyte

leukocyte that is histologically identifiable by its large nuclei; it is a small cell with very little cytoplasm

macrophage

large phagocytic cell that engulfs foreign particles and pathogens

major histocompatibility class (MHC) I/II molecule

protein found on the surface of all nucleated cells (I) or specifically on antigen-presenting cells (II) that signals to immune cells whether the cell is healthy/normal or is infected/cancerous; it provides the appropriate template into which antigens can be loaded for recognition by lymphocytes

mast cell

leukocyte that produces inflammatory molecules, such as histamine, in response to large pathogens and allergens

monocyte

type of white blood cell that circulates in the blood and lymph and differentiates into macrophages after it moves into infected tissue

natural killer (NK) cell

lymphocyte that can kill cells infected with viruses or tumor cells

neutrophil

phagocytic leukocyte that engulfs and digests pathogens

opsonization

process that enhances phagocytosis using proteins to indicate the presence of a pathogen to phagocytic cells

pathogen-associated molecular pattern (PAMP)

carbohydrate, polypeptide, and nucleic acid “signature” that is expressed by viruses, bacteria, and parasites but differs from molecules on host cells

pattern recognition receptor (PRR)

molecule on macrophages and dendritic cells

that binds molecular signatures of pathogens and promotes pathogen engulfment and destruction

perforin

destructive protein that creates a pore in the target cell; used by NK cells and killer T cells

T cell

lymphocyte that matures in the thymus gland; one of the main cells involved in the adaptive immune system

Adaptive Immune Response

By the end of this section, you will be able to:

- Explain adaptive immunity
- Compare and contrast adaptive and innate immunity
- Describe cell-mediated immune response and humoral immune response
- Describe immune tolerance

The adaptive, or acquired, immune response takes days or even weeks to become established—much longer than the innate response; however, adaptive immunity is more specific to pathogens and has memory. **Adaptive immunity** is an immunity that occurs after exposure to an antigen either from a pathogen or a vaccination. This part of the immune system is activated when the innate immune response is insufficient to control an infection. In fact, without information from the innate immune system, the adaptive response could not be mobilized. There are two types of adaptive responses: the **cell-mediated immune response**, which is carried out by T cells, and the **humoral immune response**, which is controlled by activated B cells and antibodies. Activated T cells and B cells that are specific to molecular structures on the pathogen proliferate and attack the invading pathogen. Their attack can kill pathogens directly or secrete antibodies that enhance the phagocytosis of pathogens and disrupt the infection. Adaptive

immunity also involves a memory to provide the host with long-term protection from reinfection with the same type of pathogen; on re-exposure, this memory will facilitate an efficient and quick response.

An APC, such as a macrophage, engulfs and digests a foreign bacterium. An antigen from the bacterium is presented on the cell surface in conjunction with an MHC II molecule. Lymphocytes of the adaptive immune response interact with antigen-embedded MHC II molecules to mature into functional immune cells.

Antigen-presenting Cells

Unlike NK cells of the innate immune system, B cells (B lymphocytes) are a type of white blood cell that gives rise to antibodies, whereas T cells (T lymphocytes) are a type of white blood cell that plays an important role in the immune response. T cells are a key component in the cell-mediated response—the specific immune response that utilizes T cells to neutralize cells that have been infected with viruses and certain bacteria. There are three types of T cells: cytotoxic, helper, and suppressor T cells. Cytotoxic T cells destroy virus-infected cells in the cell-mediated immune response, and helper T cells play a part in activating both the antibody and the cell-mediated immune responses. Suppressor T cells deactivate T cells and B cells when needed, and thus prevent the immune response from becoming

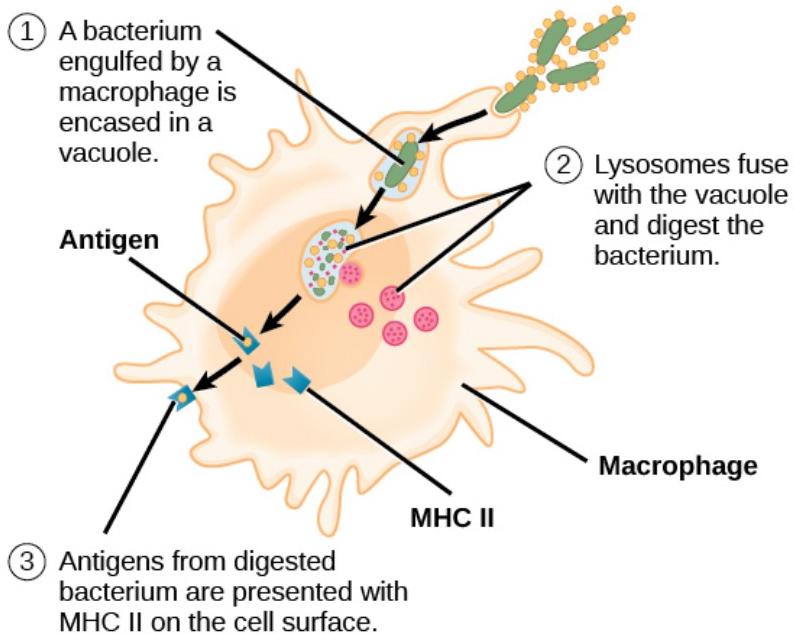
too intense.

An **antigen** is a foreign or “non-self” macromolecule that reacts with cells of the immune system. Not all antigens will provoke a response. For instance, individuals produce innumerable “self” antigens and are constantly exposed to harmless foreign antigens, such as food proteins, pollen, or dust components. The suppression of immune responses to harmless macromolecules is highly regulated and typically prevents processes that could be damaging to the host, known as tolerance.

The innate immune system contains cells that detect potentially harmful antigens, and then inform the adaptive immune response about the presence of these antigens. An **antigen-presenting cell (APC)** is an immune cell that detects, engulfs, and informs the adaptive immune response about an infection. When a pathogen is detected, these APCs will phagocytose the pathogen and digest it to form many different fragments of the antigen. Antigen fragments will then be transported to the surface of the APC, where they will serve as an indicator to other immune cells. **Dendritic cells** are immune cells that process antigen material; they are present in the skin (Langerhans cells) and the lining of the nose, lungs, stomach, and intestines. Sometimes a dendritic cell presents on the surface of other cells to induce an immune response, thus functioning as an antigen-presenting cell. Macrophages also

function as APCs. Before activation and differentiation, B cells can also function as APCs.

After phagocytosis by APCs, the phagocytic vesicle fuses with an intracellular lysosome forming phagolysosome. Within the phagolysosome, the components are broken down into fragments; the fragments are then loaded onto MHC class I or MHC class II molecules and are transported to the cell surface for antigen presentation, as illustrated in [\[link\]](#). Note that T lymphocytes cannot properly respond to the antigen unless it is processed and embedded in an MHC II molecule. APCs express MHC on their surfaces, and when combined with a foreign antigen, these complexes signal a “non-self” invader. Once the fragment of antigen is embedded in the MHC II molecule, the immune cell can respond. Helper T- cells are one of the main lymphocytes that respond to antigen-presenting cells. Recall that all other nucleated cells of the body expressed MHC I molecules, which signal “healthy” or “normal.”



Link to Learning



This [animation](#) from Rockefeller University shows how dendritic cells act as sentinels in the body's immune system.

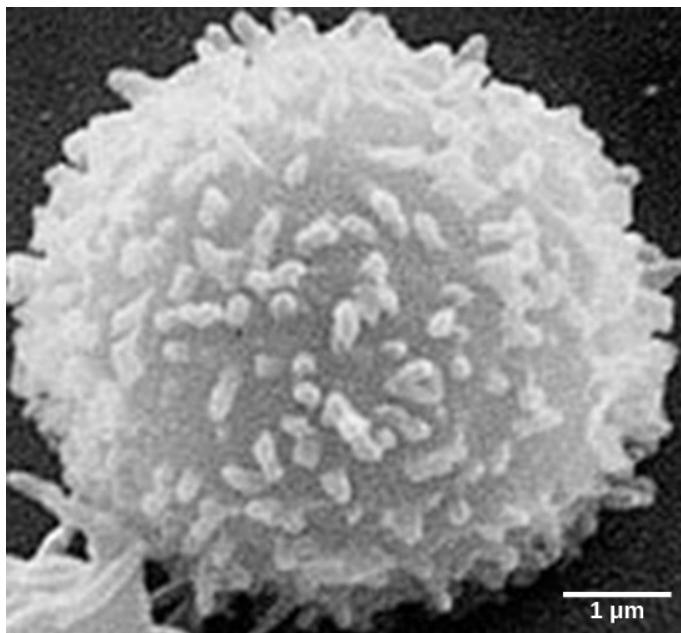
This scanning electron micrograph shows a T lymphocyte, which is responsible for the cell-mediated immune response. T cells are able to recognize antigens. (credit: modification of work by NCI; scale-bar data from Matt Russell) An antigen is a macromolecule that reacts with components of the immune system. A given antigen may contain several motifs that are recognized by immune cells. Each motif is an epitope. In this figure, the entire structure is an antigen, and the orange, salmon and green components projecting from it represent potential epitopes. A T cell receptor spans the membrane and projects variable binding regions into the extracellular space to bind processed antigens via MHC molecules on APCs. B cell receptors are embedded in the membranes of B cells and bind a variety of antigens through their variable regions. The signal transduction region transfers the signal into the cell. The topology and function of intestinal MALT is shown. Pathogens are taken up by M cells in the intestinal epithelium and excreted into a pocket formed by the inner surface of the cell. The pocket contains antigen-presenting cells such as dendritic cells, which engulf the antigens, then present them with MHC II molecules on the cell surface. The dendritic cells migrate to an underlying tissue called a Peyer's patch. Antigen-presenting cells, T cells, and B cells aggregate within the Peyer's patch, forming organized lymphoid follicles. There, some T cells and B cells are activated. Other antigen-loaded dendritic cells migrate through the

lymphatic system where they activate B cells, T cells, and plasma cells in the lymph nodes. The activated cells then return to MALT tissue effector sites. IgA and other antibodies are secreted into the intestinal lumen.

T and B Lymphocytes

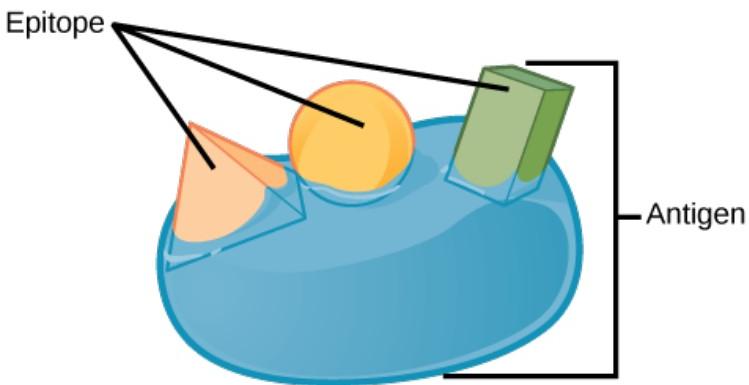
Lymphocytes in human circulating blood are approximately 80 to 90 percent T cells, shown in [\[link\]](#), and 10 to 20 percent B cells. Recall that the T cells are involved in the cell-mediated immune response, whereas B cells are part of the humoral immune response.

T cells encompass a heterogeneous population of cells with extremely diverse functions. Some T cells respond to APCs of the innate immune system, and indirectly induce immune responses by releasing cytokines. Other T cells stimulate B cells to prepare their own response. Another population of T cells detects APC signals and directly kills the infected cells. Other T cells are involved in suppressing inappropriate immune reactions to harmless or “self” antigens.



T and B cells exhibit a common theme of recognition/binding of specific antigens via a complementary receptor, followed by activation and self-amplification/maturation to specifically bind to the particular antigen of the infecting pathogen. T and B lymphocytes are also similar in that each cell only expresses one type of antigen receptor. Any individual may possess a population of T and B cells that together express a near limitless variety of antigen receptors that are capable of recognizing virtually any infecting pathogen. T and B cells are activated when they recognize small components of antigens, called **epitopes**, presented by APCs, illustrated in [\[link\]](#). Note that recognition occurs at a specific epitope rather than on the entire antigen; for this reason, epitopes are known as “antigenic

determinants.” In the absence of information from APCs, T and B cells remain inactive, or naïve, and are unable to prepare an immune response. The requirement for information from the APCs of innate immunity to trigger B cell or T cell activation illustrates the essential nature of the innate immune response to the functioning of the entire immune system.

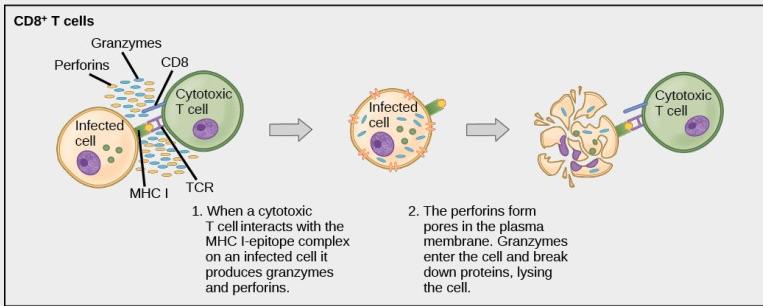
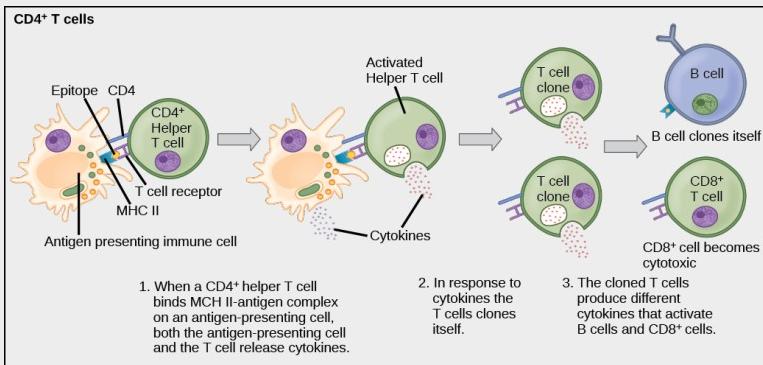


Naïve T cells can express one of two different molecules, CD4 or CD8, on their surface, as shown in [\[link\]](#), and are accordingly classified as CD4+ or CD8+ cells. These molecules are important because they regulate how a T cell will interact with and respond to an APC. Naïve CD4+ cells bind APCs via their antigen-embedded MHC II molecules and are stimulated to become **helper T (Th) lymphocytes**, cells that go on to stimulate B cells (or cytotoxic T cells) directly or secrete cytokines to inform more and various target cells about the pathogenic threat. In contrast, CD8+ cells engage antigen-embedded MHC I molecules on APCs and are stimulated to become **cytotoxic T lymphocytes (CTLs)**, which

directly kill infected cells by apoptosis and emit cytokines to amplify the immune response. The two populations of T cells have different mechanisms of immune protection, but both bind MHC molecules via their antigen receptors called T cell receptors (TCRs). The CD4 or CD8 surface molecules differentiate whether the TCR will engage an MHC II or an MHC I molecule. Because they assist in binding specificity, the CD4 and CD8 molecules are described as coreceptors.

Art Connection

Naïve CD4+ T cells engage MHC II molecules on antigen-presenting cells (APCs) and become activated. Clones of the activated helper T cell, in turn, activate B cells and CD8+ T cells, which become cytotoxic T cells. Cytotoxic T cells kill infected cells.

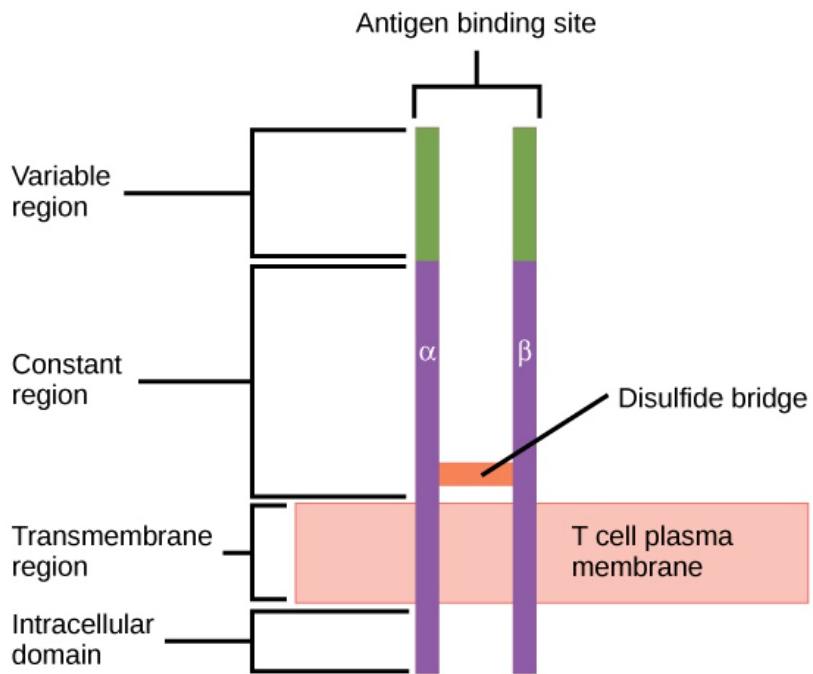


Which of the following statements about T cells is false?

- Helper T cells release cytokines while cytotoxic T cells kill the infected cell.
- Helper T cells are CD4⁺, while cytotoxic T cells are CD8⁺.
- MHC II is a receptor found on most body cells, while MHC I is a receptor found on immune cells only.
- The T cell receptor is found on both CD4⁺ and CD8⁺ T cells.

Consider the innumerable possible antigens that an

individual will be exposed to during a lifetime. The mammalian adaptive immune system is adept in responding appropriately to each antigen. Mammals have an enormous diversity of T cell populations, resulting from the diversity of TCRs. Each TCR consists of two polypeptide chains that span the T cell membrane, as illustrated in [\[link\]](#); the chains are linked by a disulfide bridge. Each polypeptide chain is comprised of a constant domain and a variable domain: a domain, in this sense, is a specific region of a protein that may be regulatory or structural. The intracellular domain is involved in intracellular signaling. A single T cell will express thousands of identical copies of one specific TCR variant on its cell surface. The specificity of the adaptive immune system occurs because it synthesizes millions of different T cell populations, each expressing a TCR that differs in its variable domain. This TCR diversity is achieved by the mutation and recombination of genes that encode these receptors in stem cell precursors of T cells. The binding between an antigen-displaying MHC molecule and a complementary TCR “match” indicates that the adaptive immune system needs to activate and produce that specific T cell because its structure is appropriate to recognize and destroy the invading pathogen.



Helper T Lymphocytes

The TH lymphocytes function indirectly to identify potential pathogens for other cells of the immune system. These cells are important for extracellular infections, such as those caused by certain bacteria, helminths, and protozoa. TH lymphocytes recognize specific antigens displayed in the MHC II complexes of APCs. There are two major populations of TH cells: TH1 and TH2. TH1 cells secrete cytokines to enhance the activities of macrophages and other T cells. TH1 cells activate the action of cytotoxic T cells, as well as macrophages. TH2 cells stimulate naïve B cells to destroy foreign invaders via antibody secretion. Whether a TH1 or a TH2 immune

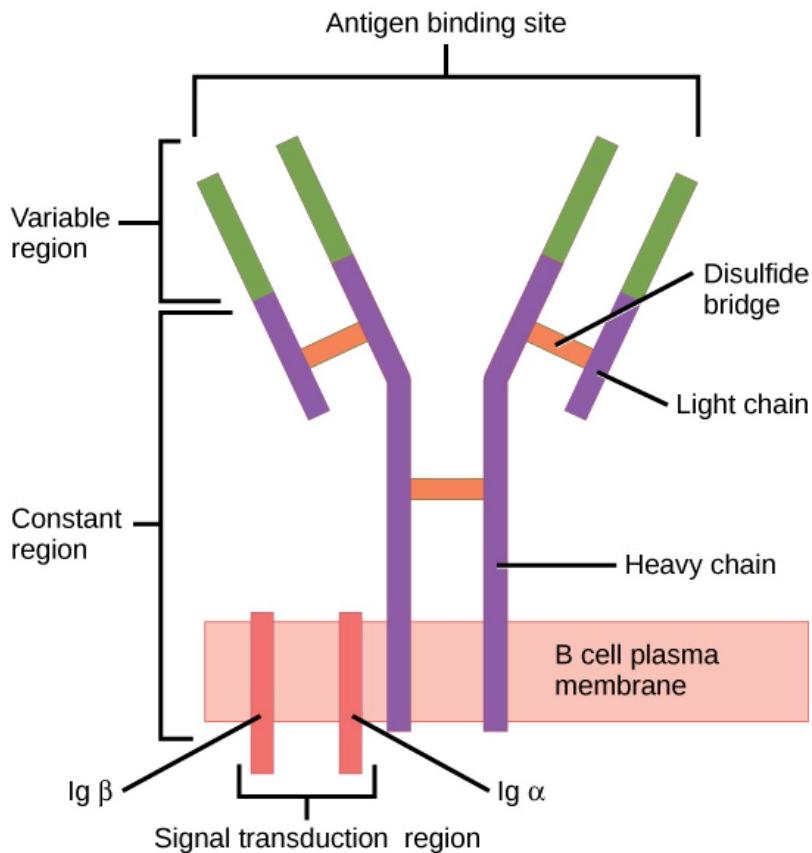
response develops depends on the specific types of cytokines secreted by cells of the innate immune system, which in turn depends on the nature of the invading pathogen.

The TH1-mediated response involves macrophages and is associated with inflammation. Recall the frontline defenses of macrophages involved in the innate immune response. Some intracellular bacteria, such as *Mycobacterium tuberculosis*, have evolved to multiply in macrophages after they have been engulfed. These pathogens evade attempts by macrophages to destroy and digest the pathogen. When *M. tuberculosis* infection occurs, macrophages can stimulate naïve T cells to become TH1 cells. These stimulated T cells secrete specific cytokines that send feedback to the macrophage to stimulate its digestive capabilities and allow it to destroy the colonizing *M. tuberculosis*. In the same manner, TH1-activated macrophages also become better suited to ingest and kill tumor cells. In summary; TH1 responses are directed toward intracellular invaders while TH2 responses are aimed at those that are extracellular.

B Lymphocytes

When stimulated by the TH2 pathway, naïve B cells differentiate into antibody-secreting plasma cells. A **plasma cell** is an immune cell that secrets antibodies; these cells arise from B cells that were

stimulated by antigens. Similar to T cells, naïve B cells initially are coated in thousands of B cell receptors (BCRs), which are membrane-bound forms of Ig (immunoglobulin, or an antibody). The B cell receptor has two heavy chains and two light chains connected by disulfide linkages. Each chain has a constant and a variable region; the latter is involved in antigen binding. Two other membrane proteins, Ig alpha and Ig beta, are involved in signaling. The receptors of any particular B cell, as shown in [\[link\]](#) are all the same, but the hundreds of millions of different B cells in an individual have distinct recognition domains that contribute to extensive diversity in the types of molecular structures to which they can bind. In this state, B cells function as APCs. They bind and engulf foreign antigens via their BCRs and then display processed antigens in the context of MHC II molecules to TH2 cells. When a TH2 cell detects that a B cell is bound to a relevant antigen, it secretes specific cytokines that induce the B cell to proliferate rapidly, which makes thousands of identical (clonal) copies of it, and then it synthesizes and secretes antibodies with the same antigen recognition pattern as the BCRs. The activation of B cells corresponding to one specific BCR variant and the dramatic proliferation of that variant is known as **clonal selection**. This phenomenon drastically, but briefly, changes the proportions of BCR variants expressed by the immune system, and shifts the balance toward BCRs specific to the infecting pathogen.



T and B cells differ in one fundamental way: whereas T cells bind antigens that have been digested and embedded in MHC molecules by APCs, B cells function as APCs that bind intact antigens that have not been processed. Although T and B cells both react with molecules that are termed “antigens,” these lymphocytes actually respond to very different types of molecules. B cells must be able to bind intact antigens because they secrete antibodies that must recognize the pathogen directly, rather than digested remnants of the

pathogen. Bacterial carbohydrate and lipid molecules can activate B cells independently from the T cells.

Cytotoxic T Lymphocytes

CTLs, a subclass of T cells, function to clear infections directly. The cell-mediated part of the adaptive immune system consists of CTLs that attack and destroy infected cells. CTLs are particularly important in protecting against viral infections; this is because viruses replicate within cells where they are shielded from extracellular contact with circulating antibodies. When APCs phagocytize pathogens and present MHC I-embedded antigens to naïve CD8+ T cells that express complementary TCRs, the CD8+ T cells become activated to proliferate according to clonal selection. These resulting CTLs then identify non-APCs displaying the same MHC I-embedded antigens (for example, viral proteins)—for example, the CTLs identify infected host cells.

Intracellularly, infected cells typically die after the infecting pathogen replicates to a sufficient concentration and lyses the cell, as many viruses do. CTLs attempt to identify and destroy infected cells before the pathogen can replicate and escape, thereby halting the progression of intracellular infections. CTLs also support NK lymphocytes to destroy early cancers. Cytokines secreted by the Th1

response that stimulates macrophages also stimulate CTLs and enhance their ability to identify and destroy infected cells and tumors.

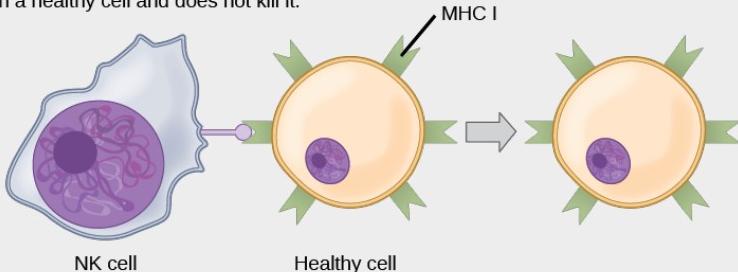
CTLs sense MHC I-embedded antigens by directly interacting with infected cells via their TCRs.

Binding of TCRs with antigens activates CTLs to release perforin and granzyme, degradative enzymes that will induce apoptosis of the infected cell. Recall that this is a similar destruction mechanism to that used by NK cells. In this process, the CTL does not become infected and is not harmed by the secretion of perforin and granzymes. In fact, the functions of NK cells and CTLs are complementary and maximize the removal of infected cells, as illustrated in [\[link\]](#). If the NK cell cannot identify the “missing self” pattern of down-regulated MHC I molecules, then the CTL can identify it by the complex of MHC I with foreign antigens, which signals “altered self.” Similarly, if the CTL cannot detect antigen-embedded MHC I because the receptors are depleted from the cell surface, NK cells will destroy the cell instead. CTLs also emit cytokines, such as interferons, that alter surface protein expression in other infected cells, such that the infected cells can be easily identified and destroyed. Moreover, these interferons can also prevent virally infected cells from releasing virus particles.

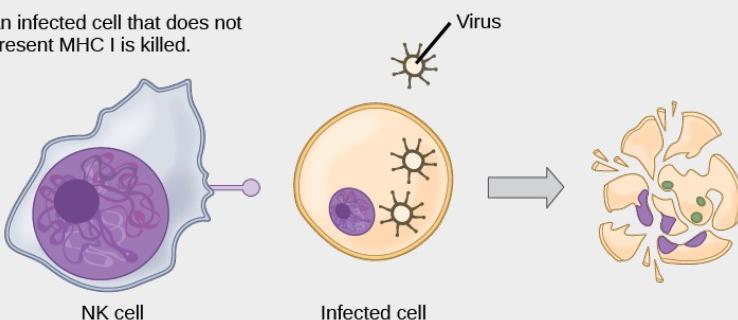
Art Connection

Natural killer (NK) cells recognize the MHC I receptor on healthy cells. If MHC I is absent, the cell is lysed.

A natural killer (NK) cell recognizes MHC I on a healthy cell and does not kill it.



An infected cell that does not present MHC I is killed.



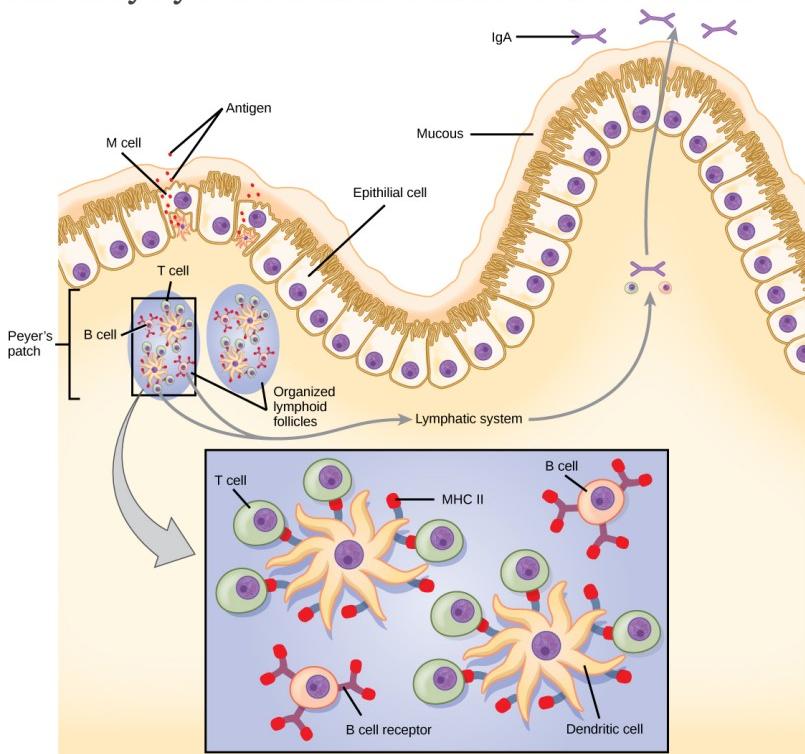
Based on what you know about MHC receptors, why do you think an organ transplanted from an incompatible donor to a recipient will be rejected?

Plasma cells and CTLs are collectively called **effector cells**: they represent differentiated versions of their naïve counterparts, and they are involved in bringing about the immune defense of killing pathogens and infected host cells.

Mucosal Surfaces and Immune Tolerance

The innate and adaptive immune responses discussed thus far comprise the systemic immune system (affecting the whole body), which is distinct from the mucosal immune system. Mucosal immunity is formed by mucosa-associated lymphoid tissue, which functions independently of the systemic immune system, and which has its own innate and adaptive components. **Mucosa-associated lymphoid tissue (MALT)**, illustrated in [\[link\]](#), is a collection of lymphatic tissue that combines with epithelial tissue lining the mucosa throughout the body. This tissue functions as the immune barrier and response in areas of the body with direct contact to the external environment. The systemic and mucosal immune systems use many of the same cell types. Foreign particles that make their way to MALT are taken up by absorptive epithelial cells called M cells and delivered to APCs located directly below the mucosal tissue. M cells function in the transport described, and are located in the Peyer's patch, a lymphoid nodule. APCs of the mucosal immune system are primarily dendritic cells, with B cells and macrophages having minor roles. Processed antigens displayed on APCs are detected by T cells in the MALT and at various mucosal induction sites, such as the tonsils, adenoids, appendix, or the mesenteric lymph nodes of the intestine. Activated T cells then migrate through the lymphatic system and into the

circulatory system to mucosal sites of infection.



MALT is a crucial component of a functional immune system because mucosal surfaces, such as the nasal passages, are the first tissues onto which inhaled or ingested pathogens are deposited. The mucosal tissue includes the mouth, pharynx, and esophagus, and the gastrointestinal, respiratory, and urogenital tracts.

The immune system has to be regulated to prevent wasteful, unnecessary responses to harmless substances, and more importantly so that it does not attack “self.” The acquired ability to prevent an unnecessary or harmful immune response to a

detected foreign substance known not to cause disease is described as **immune tolerance**. Immune tolerance is crucial for maintaining mucosal homeostasis given the tremendous number of foreign substances (such as food proteins) that APCs of the oral cavity, pharynx, and gastrointestinal mucosa encounter. Immune tolerance is brought about by specialized APCs in the liver, lymph nodes, small intestine, and lung that present harmless antigens to an exceptionally diverse population of **regulatory T (Treg) cells**, specialized lymphocytes that suppress local inflammation and inhibit the secretion of stimulatory immune factors. The combined result of Treg cells is to prevent immunologic activation and inflammation in undesired tissue compartments and to allow the immune system to focus on pathogens instead. In addition to promoting immune tolerance of harmless antigens, other subsets of Treg cells are involved in the prevention of the **autoimmune response**, which is an inappropriate immune response to host cells or self-antigens. Another Treg class suppresses immune responses to harmful pathogens after the infection has cleared to minimize host cell damage induced by inflammation and cell lysis.

In the primary response to infection, antibodies are secreted first from plasma cells. Upon re-exposure to the same pathogen, memory cells differentiate into antibody-secreting plasma cells that output a greater amount of antibody for a longer period of time.

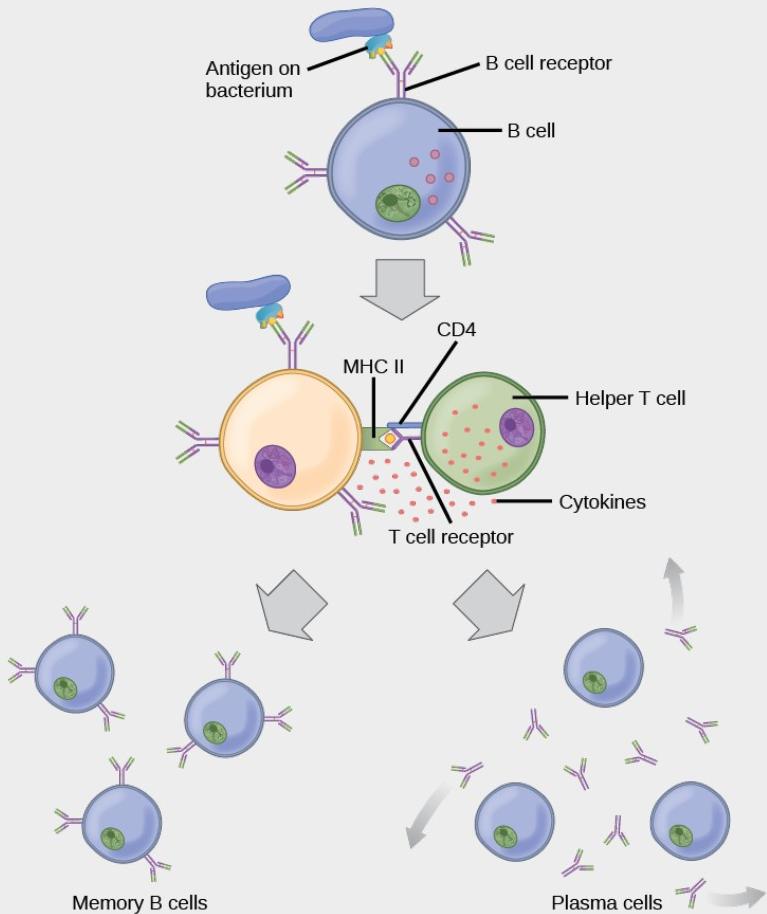
Immunological Memory

The adaptive immune system possesses a memory component that allows for an efficient and dramatic response upon reinvasion of the same pathogen. Memory is handled by the adaptive immune system with little reliance on cues from the innate response. During the adaptive immune response to a pathogen that has not been encountered before, called a primary response, plasma cells secreting antibodies and differentiated T cells increase, then plateau over time. As B and T cells mature into effector cells, a subset of the naïve populations differentiates into B and T memory cells with the same antigen specificities, as illustrated in [\[link\]](#).

A **memory cell** is an antigen-specific B or T lymphocyte that does not differentiate into effector cells during the primary immune response, but that can immediately become effector cells upon re-exposure to the same pathogen. During the primary immune response, memory cells do not respond to antigens and do not contribute to host defenses. As the infection is cleared and pathogenic stimuli subside, the effectors are no longer needed, and they undergo apoptosis. In contrast, the memory cells persist in the circulation.

Art Connection

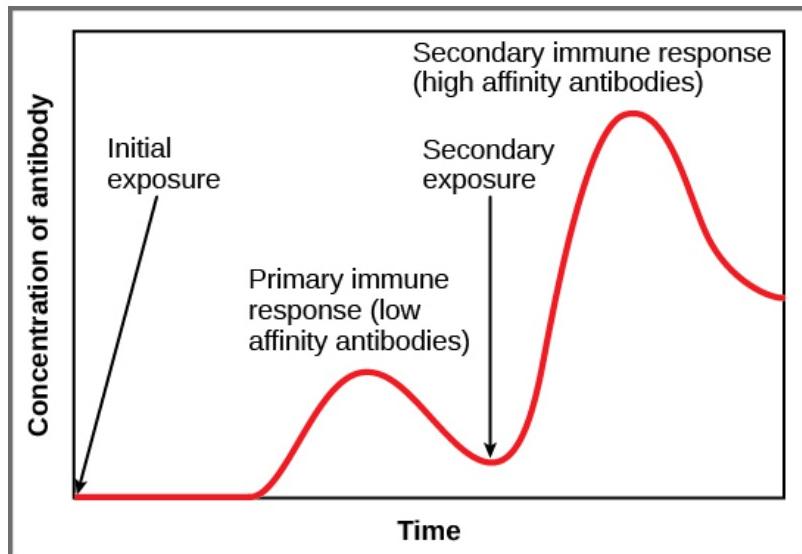
After initially binding an antigen to the B cell receptor (BCR), a B cell internalizes the antigen and presents it on MHC II. A helper T cell recognizes the MHC II–antigen complex and activates the B cell. As a result, memory B cells and plasma cells are made.



The Rh antigen is found on Rh-positive red blood cells. An Rh-negative female can usually carry an Rh-positive fetus to term without difficulty. However, if she has a second Rh-positive fetus, her body may launch an immune attack that causes

hemolytic disease of the newborn. Why do you think hemolytic disease is only a problem during the second or subsequent pregnancies?

If the pathogen is never encountered again during the individual's lifetime, B and T memory cells will circulate for a few years or even several decades and will gradually die off, having never functioned as effector cells. However, if the host is re-exposed to the same pathogen type, circulating memory cells will immediately differentiate into plasma cells and CTLs without input from APCs or TH cells. One reason the adaptive immune response is delayed is because it takes time for naïve B and T cells with the appropriate antigen specificities to be identified and activated. Upon reinfection, this step is skipped, and the result is a more rapid production of immune defenses. Memory B cells that differentiate into plasma cells output tens to hundreds-fold greater antibody amounts than were secreted during the primary response, as the graph in [\[link\]](#) illustrates. This rapid and dramatic antibody response may stop the infection before it can even become established, and the individual may not realize they had been exposed.



Vaccination is based on the knowledge that exposure to noninfectious antigens, derived from known pathogens, generates a mild primary immune response. The immune response to vaccination may not be perceived by the host as illness but still confers immune memory. When exposed to the corresponding pathogen to which an individual was vaccinated, the reaction is similar to a secondary exposure. Because each reinfection generates more memory cells and increased resistance to the pathogen, and because some memory cells die, certain vaccine courses involve one or more booster vaccinations to mimic repeat exposures: for instance, tetanus boosters are necessary every ten years because the memory cells only live that long.

Mucosal Immune Memory

A subset of T and B cells of the mucosal immune system differentiates into memory cells just as in the systemic immune system. Upon reinvasion of the same pathogen type, a pronounced immune response occurs at the mucosal site where the original pathogen deposited, but a collective defense is also organized within interconnected or adjacent mucosal tissue. For instance, the immune memory of an infection in the oral cavity would also elicit a response in the pharynx if the oral cavity was exposed to the same pathogen.

Career Connection

Vaccinologist

Vaccination (or immunization) involves the delivery, usually by injection as shown in [\[link\]](#), of noninfectious antigen(s) derived from known pathogens. Other components, called adjuvants, are delivered in parallel to help stimulate the immune response. Immunological memory is the reason vaccines work. Ideally, the effect of vaccination is to elicit immunological memory, and thus resistance to specific pathogens without the individual having to experience an infection.

Vaccines are often delivered by injection into the arm. (credit: U.S. Navy Photographer's Mate Airman Apprentice Christopher D. Blachly)



Vaccinologists are involved in the process of vaccine development from the initial idea to the availability of the completed vaccine. This process can take decades, can cost millions of dollars, and can involve many obstacles along the way. For instance, injected vaccines stimulate the systemic immune system, eliciting humoral and cell-mediated immunity, but have little effect on the mucosal response, which presents a challenge because many pathogens are deposited and replicate in mucosal compartments, and the injection does not provide the most efficient immune memory for these disease agents. For this reason, vaccinologists are actively involved in developing new vaccines that are applied via intranasal, aerosol, oral, or transcutaneous (absorbed through the skin) delivery methods. Importantly, mucosal-administered vaccines elicit both mucosal and systemic immunity and produce the same level of disease resistance as injected

vaccines.

The polio vaccine can be administered orally.
(credit: modification of work by UNICEF Sverige)



Currently, a version of intranasal influenza vaccine is available, and the polio and typhoid vaccines can be administered orally, as shown in [\[link\]](#).

Similarly, the measles and rubella vaccines are being adapted to aerosol delivery using inhalation devices. Eventually, transgenic plants may be engineered to produce vaccine antigens that can be eaten to confer disease resistance. Other vaccines may be adapted to rectal or vaginal application to elicit immune responses in rectal, genitourinary, or

reproductive mucosa. Finally, vaccine antigens may be adapted to transdermal application in which the skin is lightly scraped and microneedles are used to pierce the outermost layer. In addition to mobilizing the mucosal immune response, this new generation of vaccines may end the anxiety associated with injections and, in turn, improve patient participation.

(a) Lymphatic vessels carry a clear fluid called lymph throughout the body. The liquid enters (b) lymph nodes through afferent vessels. Lymph nodes are filled with lymphocytes that purge infecting cells. The lymph then exits through efferent vessels. (credit: modification of work by NIH, NCI) The spleen is similar to a lymph node but is much larger and filters blood instead of lymph. Blood enters the spleen through arteries and exits through veins. The spleen contains two types of tissue: red pulp and white pulp. Red pulp consists of cavities that store blood. Within the red pulp, damaged red blood cells are removed and replaced by new ones. White pulp is rich in lymphocytes that remove antigen-coated bacteria from the blood. (credit: modification of work by NCI)

Primary Centers of the Immune System

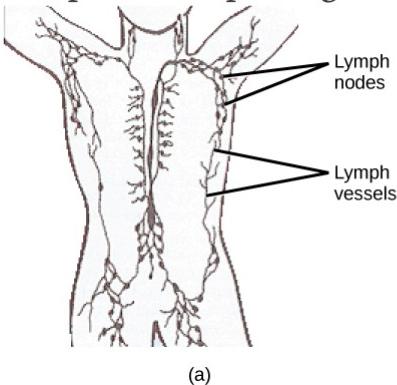
Although the immune system is characterized by

circulating cells throughout the body, the regulation, maturation, and intercommunication of immune factors occur at specific sites. The blood circulates immune cells, proteins, and other factors through the body. Approximately 0.1 percent of all cells in the blood are leukocytes, which encompass monocytes (the precursor of macrophages) and lymphocytes. The majority of cells in the blood are erythrocytes (red blood cells). **Lymph** is a watery fluid that bathes tissues and organs with protective white blood cells and does not contain erythrocytes. Cells of the immune system can travel between the distinct lymphatic and blood circulatory systems, which are separated by interstitial space, by a process called extravasation (passing through to surrounding tissue).

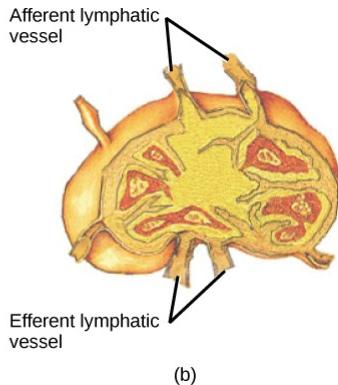
The cells of the immune system originate from hematopoietic stem cells in the bone marrow. Cytokines stimulate these stem cells to differentiate into immune cells. B cell maturation occurs in the bone marrow, whereas naïve T cells transit from the bone marrow to the thymus for maturation. In the thymus, immature T cells that express TCRs complementary to self-antigens are destroyed. This process helps prevent autoimmune responses.

On maturation, T and B lymphocytes circulate to various destinations. Lymph nodes scattered throughout the body, as illustrated in [\[link\]](#), house large populations of T and B cells, dendritic cells,

and macrophages. Lymph gathers antigens as it drains from tissues. These antigens then are filtered through lymph nodes before the lymph is returned to circulation. APCs in the lymph nodes capture and process antigens and inform nearby lymphocytes about potential pathogens.

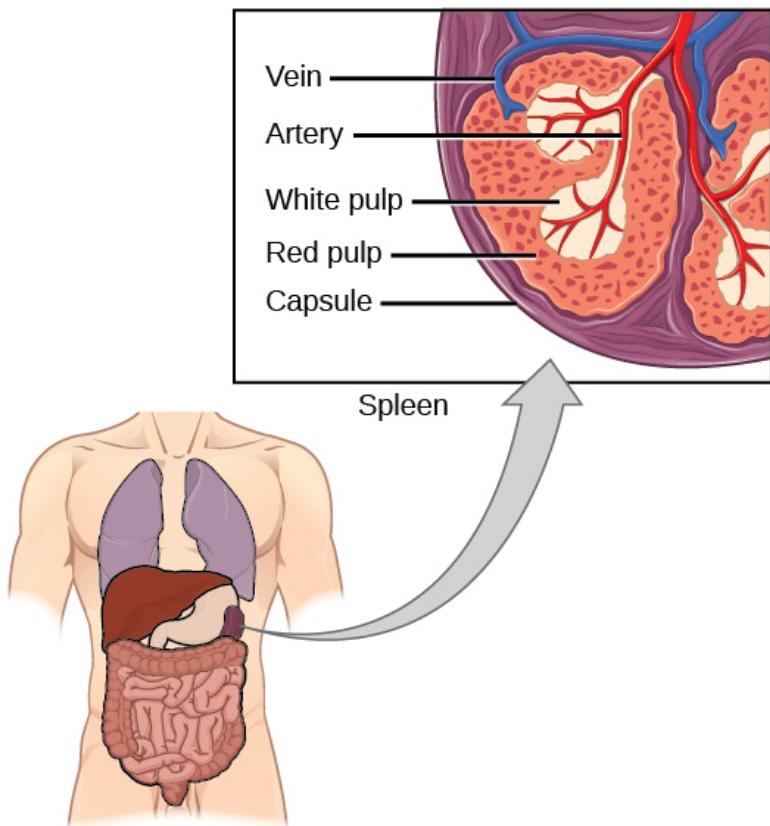


(a)



(b)

The spleen houses B and T cells, macrophages, dendritic cells, and NK cells. The spleen, shown in [\[link\]](#), is the site where APCs that have trapped foreign particles in the blood can communicate with lymphocytes. Antibodies are synthesized and secreted by activated plasma cells in the spleen, and the spleen filters foreign substances and antibody-complexed pathogens from the blood. Functionally, the spleen is to the blood as lymph nodes are to the lymph.



Section Summary

The adaptive immune response is a slower-acting, longer-lasting, and more specific response than the innate response. However, the adaptive response requires information from the innate immune system to function. APCs display antigens via MHC molecules to complementary naïve T cells. In response, the T cells differentiate and proliferate, becoming TH cells or CTLs. TH cells stimulate B cells

that have engulfed and presented pathogen-derived antigens. B cells differentiate into plasma cells that secrete antibodies, whereas CTLs induce apoptosis in intracellularly infected or cancerous cells. Memory cells persist after a primary exposure to a pathogen. If re-exposure occurs, memory cells differentiate into effector cells without input from the innate immune system. The mucosal immune system is largely independent from the systemic immune system but functions in a parallel fashion to protect the extensive mucosal surfaces of the body.

Art Connections

[\[link\]](#) Which of the following statements about T cells is false?

1. Helper T cells release cytokines while cytotoxic T cells kill the infected cell.
2. Helper T cells are CD4 +, while cytotoxic T cells are CD8 +.
3. MHC II is a receptor found on most body cells, while MHC I is a receptor found on immune cells only.
4. The T cell receptor is found on both CD4 + and CD8 + T cells.

[\[link\]](#) C

[\[link\]](#) Based on what you know about MHC receptors, why do you think an organ transplanted from an incompatible donor to a recipient will be rejected?

[\[link\]](#) MHC receptors differ from person to person. Thus, MHC receptors on an incompatible donor are considered “non-self” and are rejected by the immune system.

[\[link\]](#) The Rh antigen is found on Rh-positive red blood cells. An Rh-negative female can usually carry an Rh-positive fetus to term without difficulty. However, if she has a second Rh-positive fetus, her body may launch an immune attack that causes hemolytic disease of the newborn. Why do you think hemolytic disease is only a problem during the second or subsequent pregnancies?

[\[link\]](#) If the blood of the mother and fetus mixes, memory cells that recognize the Rh antigen can form late in the first pregnancy. During subsequent pregnancies, these memory cells launch an immune attack on the fetal blood cells. Injection of anti-Rh antibody during the first pregnancy prevents the immune

response from occurring.

Review Questions

Which of the following is both a phagocyte and an antigen-presenting cell?

1. NK cell
 2. eosinophil
 3. neutrophil
 4. macrophage
-

D

Which immune cells bind MHC molecules on APCs via CD8 coreceptors on their cell surfaces?

1. TH cells
 2. CTLs
 3. mast cells
 4. basophils
-

B

What “self” pattern is identified by NK cells?

-
1. altered self
 2. missing self
 3. normal self
 4. non-self
-

B

The acquired ability to prevent an unnecessary or destructive immune reaction to a harmless foreign particle, such as a food protein, is called _____.

1. the TH2 response
 2. allergy
 3. immune tolerance
 4. autoimmunity
-

C

A memory B cell can differentiate upon re-exposure to a pathogen of which cell type?

1. CTL
 2. naïve B cell
 3. memory T cell
 4. plasma cell
-

D

Foreign particles circulating in the blood are filtered by the _____.

1. spleen
 2. lymph nodes
 3. MALT
 4. lymph
-

A

Free Response

Explain the difference between an epitope and an antigen.

An antigen is a molecule that reacts with some component of the immune response (antibody, B cell receptor, T cell receptor). An epitope is the region on the antigen through which binding with the immune component actually occurs.

What is a naïve B or T cell?

A naïve T or B cell is one that has not been activated by binding to the appropriate epitope. Naïve T and B cells cannot produce responses.

How does the TH1 response differ from the TH2 response?

The TH1 response involves the secretion of cytokines to stimulate macrophages and CTLs and improve their destruction of intracellular pathogens and tumor cells. It is associated with inflammation. The TH2 response is involved in the stimulation of B cells into plasma cells that synthesize and secrete antibodies.

In mammalian adaptive immune systems, T cell receptors are extraordinarily diverse. What function of the immune system results from this diversity, and how is this diversity achieved?

The diversity of TCRs allows the immune system to have millions of different T cells, and thereby to be specific in distinguishing antigens. This diversity arises from mutation and recombination in the genes that encode the variable regions of TCRs.

How do B and T cells differ with respect to antigens that they bind?

T cells bind antigens that have been digested and embedded in MHC molecules by APCs. In contrast, B cells function themselves as APCs to bind intact, unprocessed antigens.

Why is the immune response after reinfection much faster than the adaptive immune response after the initial infection?

Upon reinfection, the memory cells will immediately differentiate into plasma cells and CTLs without input from APCs or TH cells. In contrast, the adaptive immune response to the initial infection requires time for naïve B and T cells with the appropriate antigen specificities to be identified and activated.

Glossary

adaptive immunity

immunity that has memory and occurs after exposure to an antigen either from a pathogen or a vaccination

antigen

foreign or “non-self” protein that triggers the immune response

antigen-presenting cell (APC)

immune cell that detects, engulfs, and informs the adaptive immune response about an infection by presenting the processed antigen on the cell surface

autoimmune response

inappropriate immune response to host cells or self-antigens

cell-mediated immune response

adaptive immune response that is carried out by T cells

clonal selection

activation of B cells corresponding to one specific BCR variant and the dramatic proliferation of that variant

cytotoxic T lymphocyte (CTL)

adaptive immune cell that directly kills infected cells via perforin and granzymes, and releases cytokines to enhance the immune response

dendritic cell

immune cell that processes antigen material and presents it on the surface of other cells to induce an immune response

effector cell

lymphocyte that has differentiated, such as a B cell, plasma cell, or cytotoxic T lymphocyte

epitope

small component of an antigen that is specifically recognized by antibodies, B cells, and T cells; the antigenic determinant

helper T lymphocyte (T_H)

cell of the adaptive immune system that binds APCs via MHC II molecules and stimulates B cells or secretes cytokines to initiate the immune response

humoral immune response

adaptive immune response that is controlled by activated B cells and antibodies

immune tolerance

acquired ability to prevent an unnecessary or harmful immune response to a detected foreign body known not to cause disease or to self-antigens

lymph

watery fluid that bathes tissues and organs with protective white blood cells and does not contain erythrocytes

mucosa-associated lymphoid tissue (MALT)

collection of lymphatic tissue that combines

with epithelial tissue lining the mucosa throughout the body

memory cell

antigen-specific B or T lymphocyte that does not differentiate into effector cells during the primary immune response but that can immediately become an effector cell upon re-exposure to the same pathogen

plasma cell

immune cell that secretes antibodies; these cells arise from B cells that were stimulated by antigens

regulatory T (T_{reg}) cell

specialized lymphocyte that suppresses local inflammation and inhibits the secretion of cytokines, antibodies, and other stimulatory immune factors; involved in immune tolerance

Disruptions in the Immune System

By the end of this section, you will be able to do the following:

- Describe hypersensitivity
- Define autoimmunity

A functioning immune system is essential for survival, but even the sophisticated cellular and molecular defenses of the mammalian immune response can be defeated by pathogens at virtually every step. In the competition between immune protection and pathogen evasion, pathogens have the advantage of more rapid evolution because of their shorter generation time and other characteristics. For instance, *Streptococcus pneumoniae* (bacterium that cause pneumonia and meningitis) surrounds itself with a capsule that inhibits phagocytes from engulfing it and displaying antigens to the adaptive immune system.

Staphylococcus aureus (bacterium that can cause skin infections, abscesses, and meningitis) synthesizes a toxin called leukocidin that kills phagocytes after they engulf the bacterium. Other pathogens can also hinder the adaptive immune system. HIV infects TH cells via their CD4 surface molecules, gradually depleting the number of TH cells in the body; this inhibits the adaptive immune system's capacity to generate sufficient responses to infection or tumors. As a result, HIV-infected individuals often suffer from infections that would not cause illness in

people with healthy immune systems but which can cause devastating illness to immune-compromised individuals. Maladaptive responses of immune cells and molecules themselves can also disrupt the proper functioning of the entire system, leading to host cell damage that could become fatal.

Immunodeficiency

Failures, insufficiencies, or delays at any level of the immune response can allow pathogens or tumor cells to gain a foothold and replicate or proliferate to high enough levels that the immune system becomes overwhelmed. **Immunodeficiency** is the failure, insufficiency, or delay in the response of the immune system, which may be acquired or inherited. Immunodeficiency can be acquired as a result of infection with certain pathogens (such as HIV), chemical exposure (including certain medical treatments), malnutrition, or possibly by extreme stress. For instance, radiation exposure can destroy populations of lymphocytes and elevate an individual's susceptibility to infections and cancer. Dozens of genetic disorders result in immunodeficiencies, including Severe Combined Immunodeficiency (SCID), Bare lymphocyte syndrome, and MHC II deficiencies. Rarely, primary immunodeficiencies that are present from birth may occur. Neutropenia is one form in which the immune system produces a below-average number

of neutrophils, the body's most abundant phagocytes. As a result, bacterial infections may go unrestricted in the blood, causing serious complications.

On first exposure to an allergen, an IgE antibody is synthesized by plasma cells in response to a harmless antigen. The IgE molecules bind to mast cells, and on secondary exposure, the mast cells release histamines and other modulators that affect the symptoms of allergy. (credit: modification of work by NIH) Systemic lupus erythematosus is characterized by autoimmunity to the individual's own DNA and/or proteins, which leads to varied dysfunction of the organs. (credit: modification of work by Mikael Häggström)

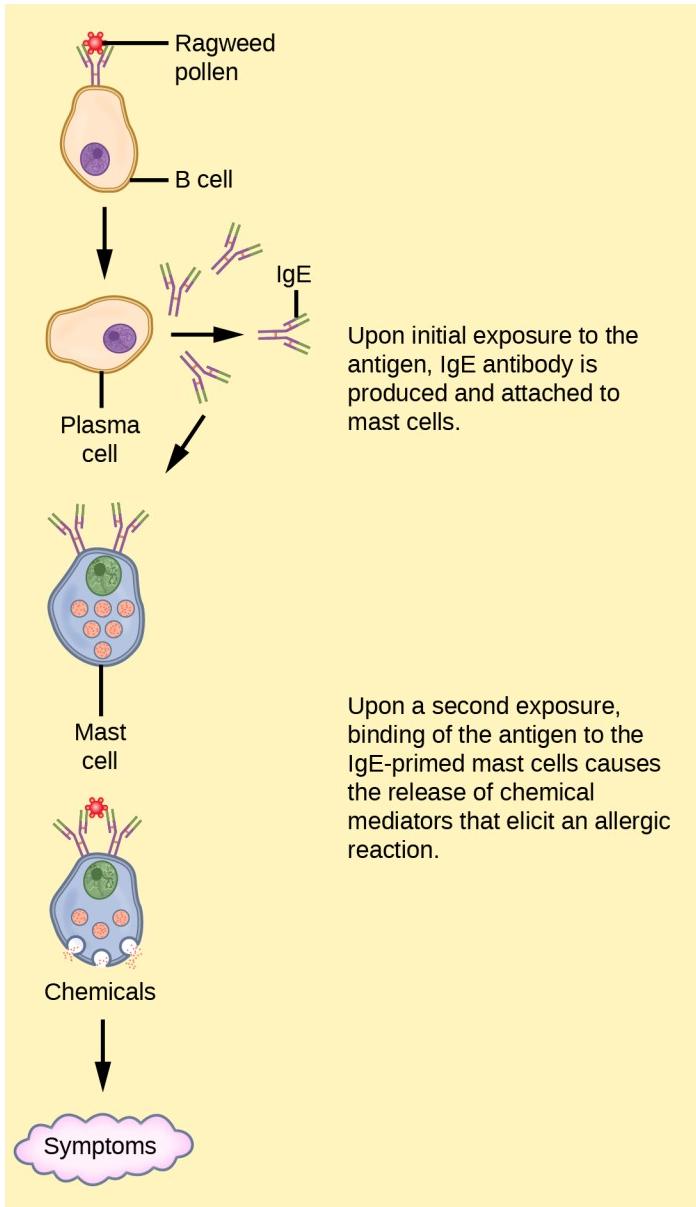
Hypersensitivities

Maladaptive immune responses toward harmless foreign substances or self antigens that occur after tissue sensitization are termed **hypersensitivities**. The types of hypersensitivities include immediate, delayed, and autoimmunity. A large proportion of the population is affected by one or more types of hypersensitivity.

Allergies

The immune reaction that results from immediate hypersensitivities in which an antibody-mediated

immune response occurs within minutes of exposure to a harmless antigen is called an **allergy**. In the United States, 20 percent of the population exhibits symptoms of allergy or asthma, whereas 55 percent test positive against one or more allergens. Upon initial exposure to a potential allergen, an allergic individual synthesizes antibodies of the IgE class via the typical process of APCs presenting processed antigen to TH cells that stimulate B cells to produce IgE. This class of antibodies also mediates the immune response to parasitic worms. The constant domain of the IgE molecules interact with mast cells embedded in connective tissues. This process primes, or sensitizes, the tissue. Upon subsequent exposure to the same allergen, IgE molecules on mast cells bind the antigen via their variable domains and stimulate the mast cell to release the modified amino acids histamine and serotonin; these chemical mediators then recruit eosinophils which mediate allergic responses. [\[link\]](#) shows an example of an allergic response to ragweed pollen. The effects of an allergic reaction range from mild symptoms like sneezing and itchy, watery eyes to more severe or even life-threatening reactions involving intensely itchy welts or hives, airway contraction with severe respiratory distress, and plummeting blood pressure. This extreme reaction is known as anaphylactic shock. If not treated with epinephrine to counter the blood pressure and breathing effects, this condition can be fatal.



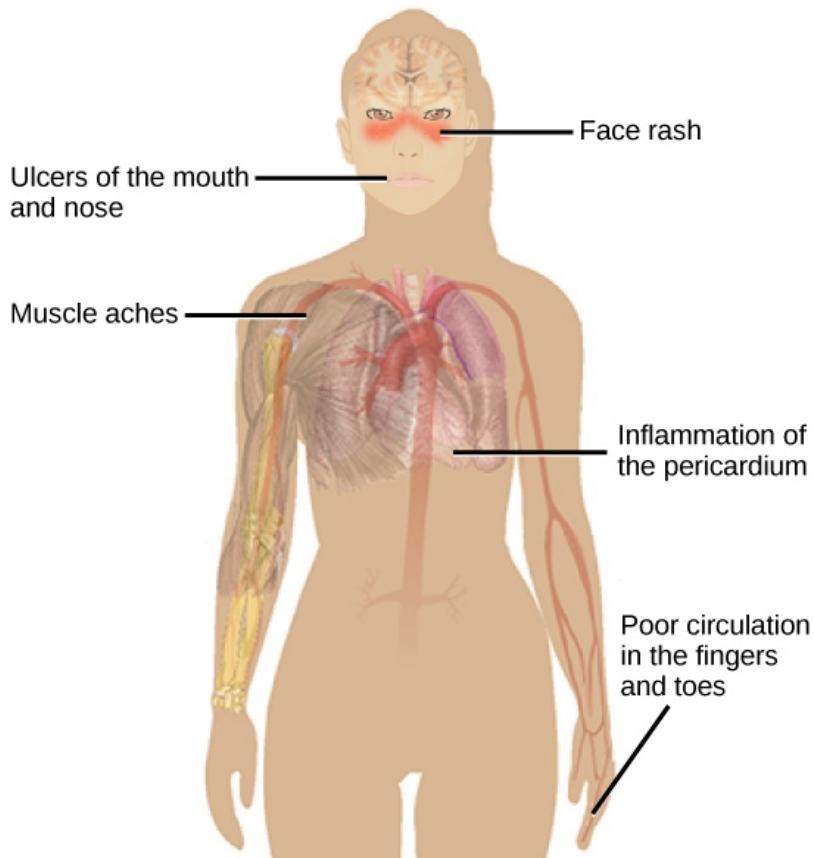
Delayed hypersensitivity is a cell-mediated immune response that takes approximately one to two days after secondary exposure for a maximal reaction to

be observed. This type of hypersensitivity involves the TH1 cytokine-mediated inflammatory response and may manifest as local tissue lesions or contact dermatitis (rash or skin irritation). Delayed hypersensitivity occurs in some individuals in response to contact with certain types of jewelry or cosmetics. Delayed hypersensitivity facilitates the immune response to poison ivy and is also the reason why the skin test for tuberculosis results in a small region of inflammation on individuals who were previously exposed to *Mycobacterium tuberculosis*. That is also why cortisone is used to treat such responses: it will inhibit cytokine production.

Autoimmunity

Autoimmunity is a type of hypersensitivity to self antigens that affects approximately five percent of the population. Most types of autoimmunity involve the humoral immune response. Antibodies that inappropriately mark self components as foreign are termed **autoantibodies**. In patients with the autoimmune disease myasthenia gravis, muscle cell receptors that induce contraction in response to acetylcholine are targeted by antibodies. The result is muscle weakness that may include marked difficulty with fine and/or gross motor functions. In systemic lupus erythematosus, a diffuse autoantibody response to the individual's own DNA and proteins results in various systemic diseases. As

illustrated in [\[link\]](#), systemic lupus erythematosus may affect the heart, joints, lungs, skin, kidneys, central nervous system, or other tissues, causing tissue damage via antibody binding, complement recruitment, lysis, and inflammation.



Autoimmunity can develop with time, and its causes may be rooted in molecular mimicry. Antibodies and TCRs may bind self antigens that are structurally similar to pathogen antigens, which the immune receptors first raised. As an example, infection with *Streptococcus pyogenes* (bacterium that

causes strep throat) may generate antibodies or T cells that react with heart muscle, which has a similar structure to the surface of *S. pyogenes*. These antibodies can damage heart muscle with autoimmune attacks, leading to rheumatic fever. Insulin-dependent (Type 1) diabetes mellitus arises from a destructive inflammatory TH1 response against insulin-producing cells of the pancreas. Patients with this autoimmunity must be injected with insulin that originates from other sources.

Section Summary

Immune disruptions may involve insufficient immune responses or inappropriate immune targets. Immunodeficiency increases an individual's susceptibility to infections and cancers. Hypersensitivities are misdirected responses either to harmless foreign particles, as in the case of allergies, or to host factors, as in the case of autoimmunity. Reactions to self components may be the result of molecular mimicry.

Review Questions

Allergy to pollen is classified as:

-
1. an autoimmune reaction
 2. immunodeficiency
 3. delayed hypersensitivity
 4. immediate hypersensitivity
-

D

A potential cause of acquired autoimmunity is _____.

1. tissue hypersensitivity
 2. molecular mimicry
 3. histamine release
 4. radiation exposure
-

B

Autoantibodies are probably involved in:

1. reactions to poison ivy
 2. pollen allergies
 3. systemic lupus erythematosus
 4. HIV/AIDS
-

C

Which of the following diseases is not due to autoimmunity?

1. rheumatic fever
 2. systemic lupus erythematosus
 3. diabetes mellitus
 4. HIV/AIDS
-

D

Glossary

allergy

immune reaction that results from immediate hypersensitivities in which an antibody-mediated immune response occurs within minutes of exposure to a harmless antigen

autoantibody

antibody that incorrectly marks “self” components as foreign and stimulates the immune response

autoimmunity

type of hypersensitivity to self antigens

hypersensitivities

spectrum of maladaptive immune responses toward harmless foreign particles or self antigens; occurs after tissue sensitization and

includes immediate-type (allergy), delayed-type, and autoimmunity

immunodeficiency

failure, insufficiency, or delay at any level of the immune system, which may be acquired or inherited

How Animals Reproduce

By the end of this section, you will be able to:

- Describe advantages and disadvantages of asexual and sexual reproduction
- Discuss asexual reproduction methods
- Discuss sexual reproduction methods
- Discuss internal and external methods of fertilization

Some animals produce offspring through asexual reproduction while other animals produce offspring through sexual reproduction. Both methods have advantages and disadvantages. **Asexual reproduction** produces offspring that are genetically identical to the parent because the offspring are all clones of the original parent. A single individual can produce offspring asexually and large numbers of offspring can be produced quickly; these are two advantages that asexually reproducing organisms have over sexually reproducing organisms. In a stable or predictable environment, asexual reproduction is an effective means of reproduction because all the offspring will be adapted to that environment. In an unstable or unpredictable environment, species that reproduce asexually may be at a disadvantage because all the offspring are genetically identical and may not be adapted to different conditions.

During **sexual reproduction**, the genetic material

of two individuals is combined to produce genetically diverse offspring that differ from their parents. The genetic diversity of sexually produced offspring is thought to give sexually reproducing individuals greater fitness because more of their offspring may survive and reproduce in an unpredictable or changing environment. Species that reproduce sexually (and have separate sexes) must maintain two different types of individuals, males and females. Only half the population (females) can produce the offspring, so fewer offspring will be produced when compared to asexual reproduction. This is a disadvantage of sexual reproduction compared to asexual reproduction.

The *Anthopleura artemisia* sea anemone can reproduce through fission. (a) Hydra reproduce asexually through budding: a bud forms on the tubular body of an adult hydra, develops a mouth and tentacles, and then detaches from its parent. The new hydra is fully developed and will find its own location for attachment. (b) Some coral, such as the *Lophelia pertusa* shown here, can reproduce through budding. (credit b: modification of work by Ed Bowlby, NOAA/Olympic Coast NMS; NOAA/OAR/Office of Ocean Exploration) (a) *Linckia multifora* is a species of sea star that can reproduce asexually via fragmentation. In this process, (b) an arm that has been shed grows into a new sea star. (credit a: modification of work by Dwayne Meadows, NOAA/NMFS/OPR)

Asexual Reproduction

Asexual reproduction occurs in prokaryotic microorganisms (bacteria and archaea) and in many eukaryotic, single-celled and multi-celled organisms. There are several ways that animals reproduce asexually, the details of which vary among individual species.

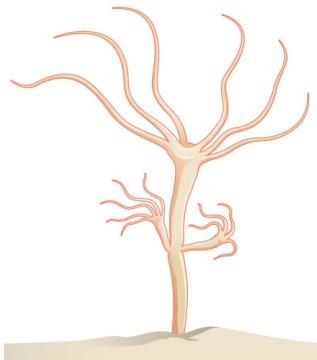
Fission

Fission, also called binary fission, occurs in some invertebrate, multi-celled organisms. It is in some ways analogous to the process of binary fission of single-celled prokaryotic organisms. The term fission is applied to instances in which an organism appears to split itself into two parts and, if necessary, regenerate the missing parts of each new organism. For example, species of turbellarian flatworms commonly called the planarians, such as *Dugesia dorotocephala*, are able to separate their bodies into head and tail regions and then regenerate the missing half in each of the two new organisms. Sea anemones (Cnidaria), such as species of the genus *Anthopleura* ([\[link\]](#)), will divide along the oral-aboral axis, and sea cucumbers (Echinodermata) of the genus *Holothuria*, will divide into two halves across the oral-aboral axis and regenerate the other half in each of the resulting individuals.



Budding

Budding is a form of asexual reproduction that results from the outgrowth of a part of the body leading to a separation of the “bud” from the original organism and the formation of two individuals, one smaller than the other. Budding occurs commonly in some invertebrate animals such as hydras and corals. In hydras, a bud forms that develops into an adult and breaks away from the main body ([\[link\]](#)).



(a)



(b)

Concept in Action

View this [video](#) to see a hydra budding.

Fragmentation

Fragmentation is the breaking of an individual into parts followed by regeneration. If the animal is capable of fragmentation, and the parts are big enough, a separate individual will regrow from each part. Fragmentation may occur through accidental damage, damage from predators, or as a natural form of reproduction. Reproduction through fragmentation is observed in sponges, some cnidarians, turbellarians, echinoderms, and annelids. In some sea stars, a new individual can be regenerated from a broken arm and a piece of the central disc. This sea star ([\[link\]](#)) is in the process of growing a complete sea star from an arm that has

been cut off. Fisheries workers have been known to try to kill the sea stars eating their clam or oyster beds by cutting them in half and throwing them back into the ocean. Unfortunately for the workers, the two parts can each regenerate a new half, resulting in twice as many sea stars to prey upon the oysters and clams.



(a)



(b)

Parthenogenesis

Parthenogenesis is a form of asexual reproduction in which an egg develops into an individual without being fertilized. The resulting offspring can be either haploid or diploid, depending on the process in the species. Parthenogenesis occurs in invertebrates such as water fleas, rotifers, aphids, stick insects, and ants, wasps, and bees. Ants, bees, and wasps use parthenogenesis to produce haploid males (drones). The diploid females (workers and queens) are the result of a fertilized egg.

Some vertebrate animals—such as certain reptiles, amphibians, and fish—also reproduce through

parthenogenesis. Parthenogenesis has been observed in species in which the sexes were separated in terrestrial or marine zoos. Two female Komodo dragons, a hammerhead shark, and a blacktop shark have produced parthenogenic young when the females have been isolated from males. It is possible that the asexual reproduction observed occurred in response to unusual circumstances and would normally not occur.

Many (a) snails are hermaphrodites. When two individuals (b) mate, they can produce up to 100 eggs each. (credit a: modification of work by Assaf Shtilman; credit b: modification of work by "Schristia"/Flickr)

Sexual Reproduction

Sexual reproduction is the combination of reproductive cells from two individuals to form genetically unique offspring. The nature of the individuals that produce the two kinds of gametes can vary, having for example separate sexes or both sexes in each individual. Sex determination, the mechanism that determines which sex an individual develops into, also can vary.

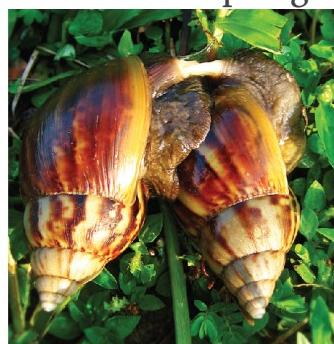
Hermaphroditism

Hermaphroditism occurs in animals in which one individual has both male and female reproductive

systems. Invertebrates such as earthworms, slugs, tapeworms, and snails ([\[link\]](#)) are often hermaphroditic. Hermaphrodites may self-fertilize, but typically they will mate with another of their species, fertilizing each other and both producing offspring. Self-fertilization is more common in animals that have limited mobility or are not motile, such as barnacles and clams. Many species have specific mechanisms in place to prevent self-fertilization, because it is an extreme form of inbreeding and usually produces less fit offspring.



(a)



(b)

Sex Determination

Mammalian sex is determined genetically by the combination of X and Y chromosomes. Individuals homozygous for X (XX) are female and heterozygous individuals (XY) are male. In mammals, the presence of a Y chromosome causes the development of male characteristics and its absence results in female characteristics. The XY system is also found in some insects and plants.

Bird sex determination is dependent on the combination of Z and W chromosomes. Homozygous for Z (ZZ) results in a male and heterozygous (ZW) results in a female. Notice that this system is the opposite of the mammalian system because in birds the female is the sex with the different sex chromosomes. The W appears to be essential in determining the sex of the individual, similar to the Y chromosome in mammals. Some fish, crustaceans, insects (such as butterflies and moths), and reptiles use the ZW system.

More complicated chromosomal sex determining systems also exist. For example, some swordtail fish have three sex chromosomes in a population.

The sex of some other species is not determined by chromosomes, but by some aspect of the environment. Sex determination in alligators, some turtles, and tuataras, for example, is dependent on the temperature during the middle third of egg development. This is referred to as environmental sex determination, or more specifically, as temperature-dependent sex determination. In many turtles, cooler temperatures during egg incubation produce males and warm temperatures produce females, while in many other species of turtles, the reverse is true. In some crocodiles and some turtles, moderate temperatures produce males and both warm and cool temperatures produce females.

Individuals of some species change their sex during their lives, switching from one to the other. If the individual is female first, it is termed protogyny or “first female,” if it is male first, it is termed protandry or “first male.” Oysters are born male, grow in size, and become female and lay eggs. The wrasses, a family of reef fishes, are all sequential hermaphrodites. Some of these species live in closely coordinated schools with a dominant male and a large number of smaller females. If the male dies, a female increases in size, changes sex, and becomes the new dominant male.

Fertilization

The fusion of a sperm and an egg is a process called fertilization. This can occur either inside (**internal fertilization**) or outside (**external fertilization**) the body of the female. Humans provide an example of the former, whereas frog reproduction is an example of the latter.

During sexual reproduction in toads, the male grasps the female from behind and externally fertilizes the eggs as they are deposited. (credit: Bernie Kohl) In (a) oviparity, young develop in eggs outside the female body, as with these *Harmonia axyridis* beetles hatching. Some aquatic animals, like this (b) pregnant *Xiphophorus maculatus* are ovoviparous, with the egg developing inside the female and nutrition supplied primarily from the

yolk. In mammals, nutrition is supported by the placenta, as was the case with this (c) newborn squirrel. (credit b: modification of work by Gourami Watcher; credit c: modification of work by "audreyjm529"/Flickr)

External Fertilization

External fertilization usually occurs in aquatic environments where both eggs and sperm are released into the water. After the sperm reaches the egg, fertilization takes place. Most external fertilization happens during the process of spawning where one or several females release their eggs and the male(s) release sperm in the same area, at the same time. The spawning may be triggered by environmental signals, such as water temperature or the length of daylight. Nearly all fish spawn, as do crustaceans (such as crabs and shrimp), mollusks (such as oysters), squid, and echinoderms (such as sea urchins and sea cucumbers). Revise to "Frogs, corals, squid, and octopuses also spawn ([\[link\]](#)).



Internal Fertilization

Internal fertilization occurs most often in terrestrial animals, although some aquatic animals also use this method. Internal fertilization may occur by the male directly depositing sperm in the female during mating. It may also occur by the male depositing sperm in the environment, usually in a protective structure, which a female picks up to deposit the sperm in her reproductive tract. There are three ways that offspring are produced following internal fertilization. In **oviparity**, fertilized eggs are laid outside the female's body and develop there, receiving nourishment from the yolk that is a part of the egg ([\[link\]a](#)). This occurs in some bony fish, some reptiles, a few cartilaginous fish, some amphibians, a few mammals, and all birds. Most non-avian reptiles and insects produce leathery eggs, while birds and some turtles produce eggs with high concentrations of calcium carbonate in

the shell, making them hard. Chicken eggs are an example of a hard shell. The eggs of the egg-laying mammals such as the platypus and echidna are leathery.

In **ovoviparity**, fertilized eggs are retained in the female, and the embryo obtains its nourishment from the egg's yolk. The eggs are retained in the female's body until they hatch inside of her, or she lays the eggs right before they hatch. This process helps protect the eggs until hatching. This occurs in some bony fish (like the platyfish *Xiphophorus maculatus*, [\[link\]b](#)), some sharks, lizards, some snakes (garter snake *Thamnophis sirtalis*), some vipers, and some invertebrate animals (Madagascar hissing cockroach *Gromphadorhina portentosa*).

In **viviparity** the young are born alive. They obtain their nourishment from the female and are born in varying states of maturity. This occurs in most mammals ([\[link\]c](#)), some cartilaginous fish, and a few reptiles.



(a)



(b)



(c)

Section Summary

Reproduction may be asexual when one individual produces genetically identical offspring, or sexual when the genetic material from two individuals is combined to produce genetically diverse offspring. Asexual reproduction in animals occurs through fission, budding, fragmentation, and parthenogenesis. Sexual reproduction may involve fertilization inside the body or in the external environment. A species may have separate sexes or combined sexes; when the sexes are combined they may be expressed at different times in the life cycle. The sex of an individual may be determined by various chromosomal systems or environmental factors such as temperature.

Sexual reproduction starts with the combination of a sperm and an egg in a process called fertilization. This can occur either outside the bodies or inside the female. The method of fertilization varies among animals. Some species release the egg and sperm into the environment, some species retain the egg and receive the sperm into the female body and then expel the developing embryo covered with shell, while still other species retain the developing offspring throughout the gestation period.

Review Questions

In which group is parthenogenesis a normal event?

1. chickens
 2. bees
 3. rabbits
 4. sea stars
-

B

Genetically unique individuals are produced through _____.

1. sexual reproduction
 2. parthenogenesis
 3. budding
 4. fragmentation
-

A

External fertilization occurs in which type of environment?

1. aquatic
 2. forested
 3. savanna
 4. steppe
-

A

Free Response

What might be a disadvantage to temperature-dependent sex determination?

Temperatures can vary from year to year and an unusually cold or hot year might produce offspring all of one sex, making it hard for individuals to find mates.

Compared to separate sexes and assuming self-fertilizing is not possible, what might be one advantage and one disadvantage to hermaphroditism?

A possible advantage of hermaphroditism might be that anytime an individual of the same species is encountered a mating is possible, unlike separate sexes that must find an individual of the right sex to mate. (Also, every individual in a hermaphrodite population is able to produce offspring, which is not the case in populations with separate sexes.) A

disadvantage might be that hermaphrodite populations are less efficient because they do not specialize in one sex or another, which means a hermaphrodite does not produce as many offspring through eggs or sperm as do species with separate sexes. (Other answers are possible.)

Glossary

asexual reproduction

a mechanism that produces offspring that are genetically identical to the parent

budding

a form of asexual reproduction that results from the outgrowth of a part of an organism leading to a separation from the original animal into two individuals

external fertilization

the fertilization of eggs by sperm outside an animal's body, often during spawning

fission

(also, binary fission) a form of asexual reproduction in which an organism splits into two separate organisms or two parts that regenerate the missing portions of the body

fragmentation

the breaking of an organism into parts and the growth of a separate individual from each part

hermaphroditism

the state of having both male and female reproductive structures within the same individual

internal fertilization

the fertilization of eggs by sperm inside the body of the female

oviparity

a process by which fertilized eggs are laid outside the female's body and develop there, receiving nourishment from the yolk that is a part of the egg

ovoviparity

a process by which fertilized eggs are retained within the female; the embryo obtains its nourishment from the egg's yolk, and the young are fully developed when they are hatched

parthenogenesis

a form of asexual reproduction in which an egg develops into a complete individual without being fertilized

sex determination

the mechanism by which the sex of individuals in sexually reproducing organisms is initially established

sexual reproduction

a form of reproduction in which cells containing genetic material from two individuals combines to produce genetically unique offspring

viviparity

a process in which the young develop within the female and are born in a nonembryonic state

Development and Organogenesis

By the end of this section, you will be able to:

- Explain how the embryo forms from the zygote
- Discuss the role of cleavage and gastrulation in animal development
- Describe organogenesis

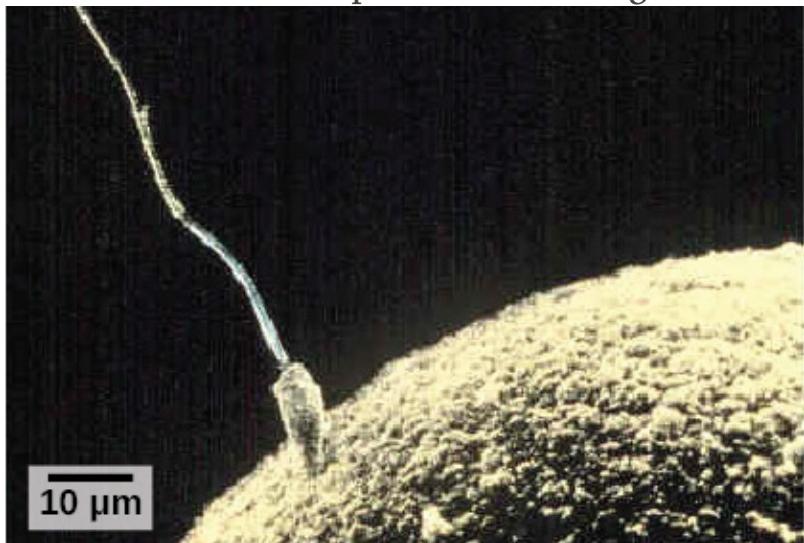
The process by which an organism develops from a single-celled zygote to a multi-cellular organism is complex and well regulated. The regulation occurs through signaling between cells and tissues and responses in the form of differential gene expression.

Fertilization is the process in which sperm and egg fuse to form a zygote. (credit: scale-bar data from Matt Russell) (a) During cleavage, the zygote rapidly divides into multiple cells. (b) The cells rearrange themselves to form a hollow ball called the blastula. (credit a: modification of work by Gray's Anatomy; credit b: modification of work by Pearson Scott Foresman; donated to the Wikimedia Foundation) Gastrulation is the process wherein the cells in the blastula rearrange themselves to form the germ layers. (credit: modification of work by Abigail Pyne)

Early Embryonic Development

Fertilization is the process in which gametes (an egg

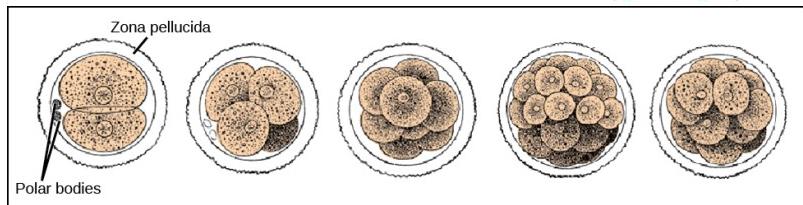
and sperm) fuse to form a zygote ([\[link\]](#)). To ensure that the offspring has only one complete diploid set of chromosomes, only one sperm must fuse with one egg. In mammals, a layer called the **zona pellucida** protects the egg. At the tip of the head of a sperm cell is a structure like a lysosome called the acrosome, which contains enzymes. When a sperm binds to the zona pellucida, a series of events, called the acrosomal reactions, take place. These reactions, involving enzymes from the acrosome, allow the sperm plasma membrane to fuse with the egg plasma membrane and permit the sperm nucleus to transfer into the ovum. The nuclear membranes of the egg and sperm break down and the two haploid nuclei fuse to form a diploid nucleus or genome.



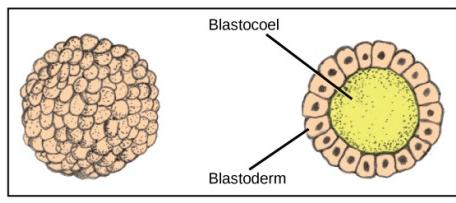
To ensure that no more than one sperm fertilizes the egg, once the acrosomal reactions take place at one location of the egg membrane, the egg releases

proteins in other locations to prevent other sperm from fusing with the egg.

The development of multi-cellular organisms begins from this single-celled zygote, which undergoes rapid cell division, called cleavage ([\[link\]a](#)), to form a hollow ball of cells called a blastula ([\[link\]b](#)).



(a)

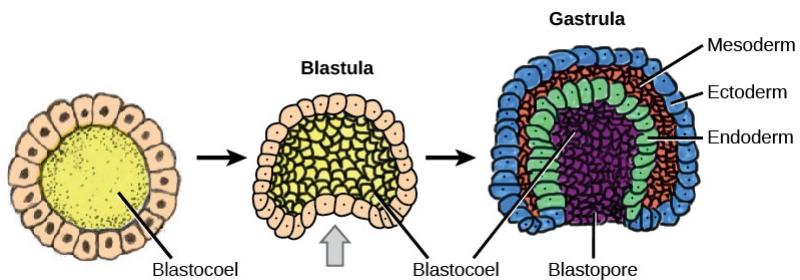


(b)

In mammals, the blastula forms the **blastocyst** in the next stage of development. Here the cells in the blastula arrange themselves in two layers: the **inner cell mass**, and an outer layer called the **trophoblast**. The inner cell mass will go on to form the embryo. The trophoblast secretes enzymes that allow implantation of the blastocyst into the endometrium of the uterus. The trophoblast will contribute to the placenta and nourish the embryo.

Visit the [Virtual Human Embryo project](#) at the Endowment for Human Development site to click through an interactive of the stages of embryo development, including micrographs and rotating 3-D images.

The cells in the blastula then rearrange themselves spatially to form three layers of cells. This process is called **gastrulation**. During gastrulation, the blastula folds in on itself and cells migrate to form the three layers of cells ([\[link\]](#)) in a structure, the gastrula, with a hollow space that will become the digestive tract. Each of the layers of cells is called a germ layer and will differentiate into different organ systems.



The three germ layers are the endoderm, the ectoderm, and the mesoderm. Cells in each germ layer differentiate into tissues and embryonic organs. The ectoderm gives rise to the nervous system and the epidermis, among other tissues. The mesoderm gives rise to the muscle cells and connective tissue in the body. The endoderm gives

rise to the gut and many internal organs.

Organogenesis

Gastrulation leads to the formation of the three germ layers that give rise during further development to the different organs in the animal body. This process is called **organogenesis**.

Organs develop from the germ layers through the process of differentiation. During differentiation, the embryonic stem cells express specific sets of genes that will determine their ultimate cell type. For example, some cells in the ectoderm will express the genes specific to skin cells. As a result, these cells will take on the shape and characteristics of epidermal cells. The process of differentiation is regulated by location-specific chemical signals from the cell's embryonic environment that sets in play a cascade of events that regulates gene expression.

Section Summary

The early stages of embryonic development begin with fertilization. The process of fertilization is tightly controlled to ensure that only one sperm fuses with one egg. After fertilization, the zygote undergoes cleavage to form the blastula. The blastula, which in some species is a hollow ball of

cells, undergoes a process called gastrulation, during which the three germ layers form. The ectoderm gives rise to the nervous system and the epidermal skin cells, the mesoderm gives rise to the muscle cells and connective tissue in the body, and the endoderm gives rise to the digestive system and other internal organs. Organogenesis is the formation of organs from the germ layers. Each germ layer gives rise to specific tissue types.

Review Questions

The process of gastrulation forms the ____.

1. blastula
 2. zygote
 3. organs
 4. germ layers
-

D

Which of the following gives rise to the skin cells?

1. ectoderm
2. endoderm
3. mesoderm

4. none of the above

A

Free Response

What do you think would happen if multiple sperm fused with one egg?

If multiple sperm fused with one egg, a zygote with a multiple ploidy level (multiple copies of the chromosomes) would form, and then would die.

Glossary

blastocyst

the structure formed when cells in the mammalian blastula separate into an inner and outer layer

gastrulation

the process in which the blastula folds over itself to form the three germ layers

inner cell mass

the inner layer of cells in the blastocyst,
which becomes the embryo

organogenesis

the process of organ formation during
development

trophoblast

the outer layer of cells in the blastocyst,
which gives rise to the embryo's contribution
to the placenta

zona pellucida

the protective layer around the mammalian
egg

Human Reproduction

By the end of this section, you will be able to:

- Describe human male and female reproductive anatomies
- Describe spermatogenesis and oogenesis and discuss their differences and similarities
- Describe the role of hormones in human reproduction
- Describe the roles of male and female reproductive hormones

As in all animals, the adaptations for reproduction in humans are complex. They involve specialized and different anatomies in the two sexes, a hormone regulation system, and specialized behaviors regulated by the brain and endocrine system.

As seen in this scanning electron micrograph, human sperm has a flagellum, neck, and head. (credit: scale-bar data from Matt Russell) The reproductive structures of the human female are shown. (credit a: modification of work by Gray's Anatomy; credit b: modification of work by CDC)

Human Reproductive Anatomy

The reproductive tissues of male and female humans develop similarly *in utero* until about the seventh week of gestation when a low level of the hormone testosterone is released from the gonads of the

developing male. Testosterone causes the primitive gonads to differentiate into male sexual organs. When testosterone is absent, the primitive gonads develop into ovaries. Tissues that produce a penis in males produce a clitoris in females. The tissue that will become the scrotum in a male becomes the labia in a female. Thus the male and female anatomies arise from a divergence in the development of what were once common embryonic structures.

Male Reproductive Anatomy

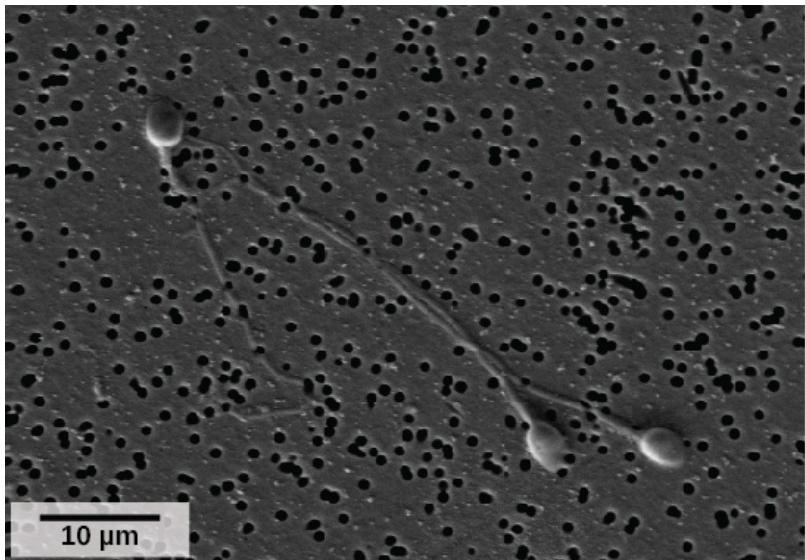
Sperm are immobile at body temperature; therefore, the testes are external to the body so that a correct temperature is maintained for motility. In land mammals, including humans, the pair of testes must be suspended outside the body so the environment of the sperm is about 2 °C lower than body temperature to produce viable sperm. If the testes do not descend through the abdominal cavity during fetal development, the individual has reduced fertility.

The **scrotum** houses the testicles or **testes** (singular: **testis**), and provides passage for blood vessels, nerves, and muscles related to testicular function. The testes are a pair of male gonads that produce sperm and reproductive hormones. Each testis is approximately 2.5 by 3.8 cm (1.5 by 1 inch) in size and divided into wedge-shaped lobes by septa.

Coiled in each wedge are seminiferous tubules that produce sperm.

The **penis** drains urine from the urinary bladder and is a copulatory organ during intercourse ([\[link\]](#); [\[link\]](#)). The penis contains three tubes of erectile tissue that become engorged with blood, making the penis erect, in preparation for intercourse. The organ is inserted into the vagina culminating with an ejaculation. During orgasm, the accessory organs and glands connected to the testes contract and empty the semen (containing sperm) into the urethra and the fluid is expelled from the body by muscular contractions causing ejaculation. After intercourse, the blood drains from the erectile tissue and the penis becomes flaccid.

Semen is a mixture of sperm (about five percent of the total) and fluids from accessory glands that contribute most of the semen's volume. Sperm are haploid cells, consisting of a flagellum for motility, a neck that contains the cell's energy-producing mitochondria, and a head that contains the genetic material ([\[link\]](#)). An acrosome (acrosomal vesicle) is found at the top of the head of the sperm. This structure contains enzymes that can digest the protective coverings that surround the egg and allow the sperm to fuse with the egg. An ejaculate will contain from two to five milliliters of fluid and from 50–120 million sperm per milliliter.



Sperm form in the walls of **seminiferous tubules** that are coiled inside the testes ([\[link\]](#); [\[link\]](#)). The walls of the seminiferous tubules are made up of the developing sperm cells, with the least developed sperm at the periphery of the tubule and the fully developed sperm next to the lumen. The sperm cells are associated with **Sertoli cells** that nourish and promote the development of the sperm. Other cells present between the walls of the tubules are the **interstitial cells of Leydig**, which produce testosterone once the male reaches adolescence.

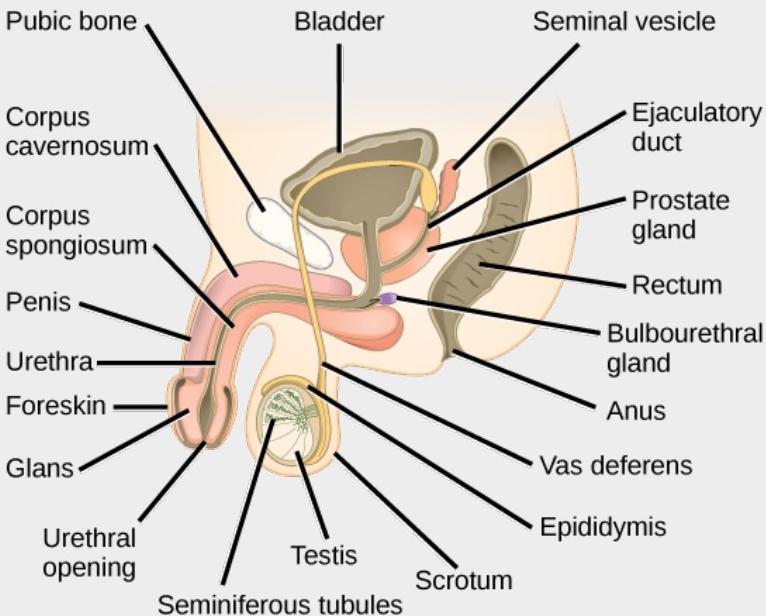
When the sperm have developed flagella they leave the seminiferous tubules and enter the epididymis ([\[link\]](#); [\[link\]](#)). This structure lies along the top and posterior of the testes and is the site of sperm maturation. The sperm leave the epididymis and enter the vas deferens, which carries the sperm

behind the bladder, and forms the ejaculatory duct with the duct from the seminal vesicles. During a vasectomy, a section of the vas deferens is removed, preventing sperm (but not the secretions of the accessory glands) from being passed out of the body during ejaculation and preventing fertilization.

The bulk of the semen comes from the accessory glands associated with the male reproductive system. These are the **seminal vesicles**, the **prostate gland**, and the **bulbourethral gland** ([\[link\]](#); [\[link\]](#)). The secretions from the accessory glands provide important compounds for the sperm including nutrients, electrolytes, and pH buffering. There are also coagulation factors that affect sperm delivery and motility.

Visual Connection

The reproductive structures of the human male are shown.



Which of the following statements about the male reproductive system is false?

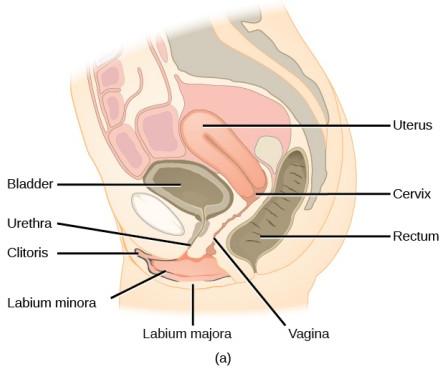
1. The vas deferens carries sperm from the testes to the seminal vesicles.
2. The ejaculatory duct joins the urethra.
3. Both the prostate and the bulbourethral glands produce components of the semen.
4. The prostate gland is located in the testes.

Male Reproductive Anatomy

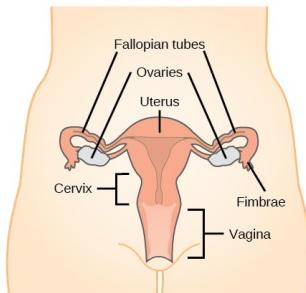
Organ	Location	Function
Scrotum	External	Supports testes and regulates their temperature
Penis	External	Delivers urine, copulating organ
Testes	Internal	Produce sperm and male hormones
Seminal Vesicles	Internal	Contribute to semen production
Prostate Gland	Internal	Contributes to semen production
Bulbourethral Glands	Internal	Neutralize urine in urethra

Female Reproductive Anatomy

A number of female reproductive structures are exterior to the body. These include the breasts and the vulva, which consists of the mons pubis, **clitoris**, **labia majora**, **labia minora**, and the vestibular glands ([\[link\]](#); [\[link\]](#)).



(a)



(b)

The breasts consist of mammary glands and fat. Each gland consists of 15 to 25 lobes that have ducts that empty at the nipple and that supply the nursing child with nutrient- and antibody-rich milk to aid development and protect the child.

Internal female reproductive structures include ovaries, oviducts, the uterus, and the vagina ([\[link\]](#); [\[link\]](#)). The pair of ovaries is held in place in the abdominal cavity by a system of ligaments. The outermost layer of the ovary is made up of follicles, each consisting of one or more follicular cells that surround, nourish, and protect a single egg. During the menstrual period, a batch of follicular cells develops and prepares their eggs for release. At ovulation, one follicle ruptures and one egg is released. Following ovulation, the follicular tissue that surrounded the ovulated egg stays within the ovary and grows to form a solid mass called the **corpus luteum**. The corpus luteum secretes additional estrogen and the hormone progesterone that helps maintain the uterine lining during

pregnancy. The ovaries also produce hormones, such as estrogen.

The **oviducts**, or fallopian tubes, extend from the uterus in the lower abdominal cavity to the ovaries, but they are not in contact with the ovaries. The lateral ends of the oviducts flare out into a trumpet-like structure and have a fringe of finger-like projections called fimbriae. When an egg is released at ovulation, the fimbriae help the nonmotile egg enter into the tube. The walls of the oviducts have a ciliated epithelium over smooth muscle. The cilia beat, and the smooth muscle contracts, moving the egg toward the uterus. Fertilization usually takes place within the oviduct and the developing embryo is moved toward the uterus. It usually takes the egg or embryo a week to travel through the oviduct.

Sterilization in women is called a tubal ligation; it is analogous to a vasectomy in males in that the oviducts are severed and sealed, preventing sperm from reaching the egg.

The **uterus** is a structure about the size of a woman's fist. The uterus has a thick muscular wall and is lined with an endometrium rich in blood vessels and mucus glands that develop and thicken during the female cycle. Thickening of the endometrium prepares the uterus to receive the fertilized egg or zygote, which will then implant itself in the endometrium. The uterus supports the

developing embryo and fetus during gestation. Contractions of the smooth muscle in the uterus aid in forcing the baby through the vagina during labor. If fertilization does not occur, a portion of the lining of the uterus sloughs off during each menstrual period. The endometrium builds up again in preparation for implantation. Part of the uterus, called the cervix, protrudes into the top of the vagina.

The **vagina** is a muscular tube that serves several purposes. It allows menstrual flow to leave the body. It is the receptacle for the penis during intercourse and the pathway for the delivery of offspring.

Female Reproductive Anatomy

Organ

Clitoris

Mons pubis

Location

External

External

Function

Sensory organ

Fatty area
overlying pubic
bone

Labia majora

External

Covers labia
minora; contains
sweat and

Labia minora	External	sebaceous glands Covers vestibule
Greater vestibular glands	External	Secrete mucus; lubricate vagina
Breast	External	Produces and delivers milk
Ovaries	Internal	Produce and develop eggs
Oviducts	Internal	Transport egg to uterus; site of fertilization
Uterus	Internal	Supports developing embryo
Vagina	Internal	Common tube for intercourse, birth canal, passing menstrual flow

During spermatogenesis, four sperm result from each primary spermatocyte. The process also maps onto the physical structure of the wall of the seminiferous tubule, with the spermatogonia on the outer side of the tubule, and the sperm with their developing tails extended into the lumen of the tubule. The process of oogenesis occurs in the ovary's outermost layer.

Gametogenesis (Spermatogenesis and Oogenesis)

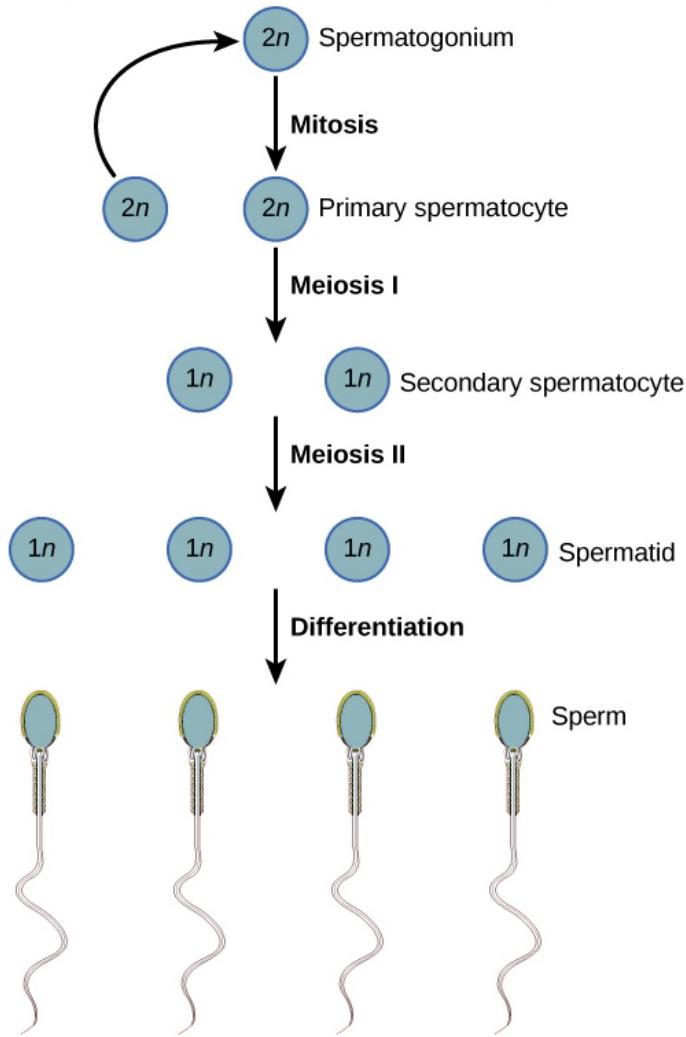
Gametogenesis, the production of sperm and eggs, involves the process of meiosis. During meiosis, two nuclear divisions separate the paired chromosomes in the nucleus and then separate the chromatids that were made during an earlier stage of the cell's life cycle. Meiosis and its associated cell divisions produces haploid cells with half of each pair of chromosomes normally found in diploid cells. The production of sperm is called **spermatogenesis** and the production of eggs is called **oogenesis**.

Spermatogenesis

Spermatogenesis occurs in the wall of the seminiferous tubules, with the most primitive cells at the periphery of the tube and the most mature sperm at the lumen of the tube ([\[link\]](#)). Immediately under the capsule of the tubule are diploid, undifferentiated cells. These stem cells, each called a spermatogonium (pl. spermatogonia), go through mitosis to produce one cell that remains as a stem cell and a second cell called a primary spermatocyte that will undergo meiosis to produce sperm.

The diploid primary spermatocyte goes through meiosis I to produce two haploid cells called secondary spermatocytes. Each secondary spermatocyte divides after meiosis II to produce two cells called spermatids. The spermatids eventually reach the lumen of the tubule and grow a flagellum, becoming sperm cells. Four sperm result from each

primary spermatocyte that goes through meiosis.

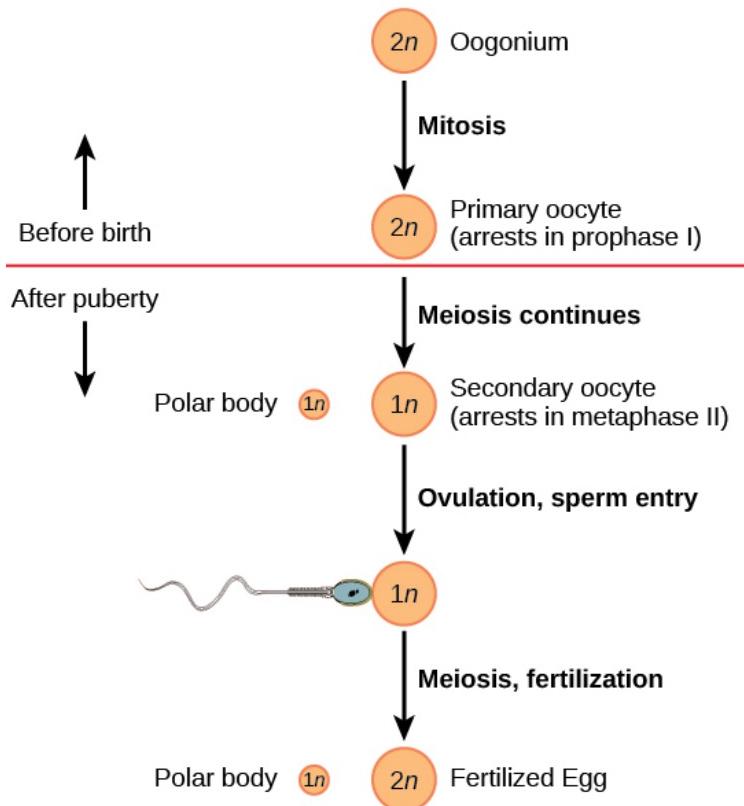


Concept in Action

Visit [this site](#) to see the process of spermatogenesis.

Oogenesis

Oogenesis occurs in the outermost layers of the ovaries. As with sperm production, oogenesis starts with a germ cell. In oogenesis, this germ cell is called an oogonium and forms during the embryological development of the individual. The oogonium undergoes mitosis to produce about one to two million oocytes by the time of birth.



The primary oocytes begin meiosis before birth ([\[link\]](#)). However, the meiotic division is arrested in its progress in the first prophase stage. At the time

of birth, all future eggs are in prophase I. This situation is in contrast with the male reproductive system in which sperm are produced continuously throughout the life of the individual. Starting at adolescence, anterior pituitary hormones cause the development of a few follicles in an ovary each month. This results in a primary oocyte finishing the first meiotic division. The cell divides unequally, with most of the cytoplasm and organelles going to one cell, called a secondary oocyte, and only one set of chromosomes and a small amount of cytoplasm going to the other cell. This second cell is called a polar body and usually dies. Cell division is again arrested, this time at metaphase II. At ovulation, this secondary oocyte is released and travels toward the uterus through the oviduct. If the secondary oocyte is fertilized, the cell continues through meiosis II, producing a second polar body and haploid egg, which fuses with the haploid sperm to form a fertilized egg (zygote) containing all 46 chromosomes.

Hormones control sperm production in a negative feedback system.

Hormonal Control of Reproduction

The human male and female reproductive cycles are controlled by the interaction of hormones from the hypothalamus and anterior pituitary with hormones from reproductive tissues and organs. In both sexes, the hypothalamus monitors and causes the release

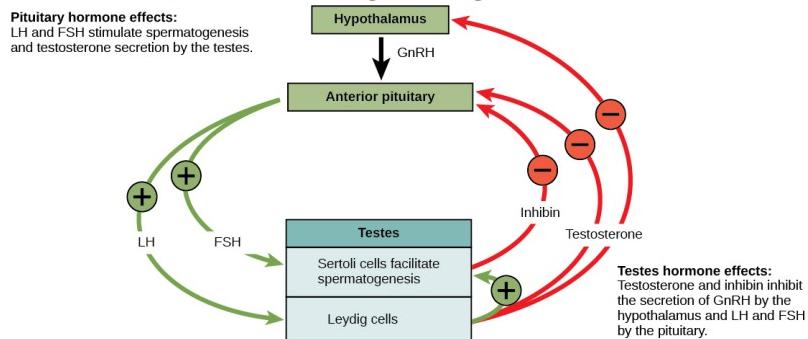
of hormones from the anterior pituitary gland. When the reproductive hormone is required, the hypothalamus sends a **gonadotropin-releasing hormone (GnRH)** to the anterior pituitary. This causes the release of **follicle stimulating hormone (FSH)** and **luteinizing hormone (LH)** from the anterior pituitary into the blood. Although these hormones are named after their functions in female reproduction, they are produced in both sexes and play important roles in controlling reproduction. Other hormones have specific functions in the male and female reproductive systems.

Male Hormones

At the onset of puberty, the hypothalamus causes the release of FSH and LH into the male system for the first time. FSH enters the testes and stimulates the Sertoli cells located in the walls of the seminiferous tubules to begin promoting spermatogenesis ([\[link\]](#)). LH also enters the testes and stimulates the interstitial cells of Leydig, located in between the walls of the seminiferous tubules, to make and release testosterone into the testes and the blood.

Testosterone stimulates spermatogenesis. This hormone is also responsible for the secondary sexual characteristics that develop in the male during adolescence. The secondary sex characteristics in males include a deepening of the voice, the growth

of facial, axillary, and pubic hair, an increase in muscle bulk, and the beginnings of the sex drive.



A negative feedback system occurs in the male with rising levels of testosterone acting on the hypothalamus and anterior pituitary to inhibit the release of GnRH, FSH, and LH. In addition, the Sertoli cells produce the hormone **inhibin**, which is released into the blood when the sperm count is too high. This inhibits the release of GnRH and FSH, which will cause spermatogenesis to slow down. If the sperm count reaches a low of 20 million/mL, the Sertoli cells cease the release of inhibin, and the sperm count increases.

Female Hormones

The control of reproduction in females is more complex. The female reproductive cycle is divided into the ovarian cycle and the menstrual cycle. The **ovarian cycle** governs the preparation of endocrine tissues and release of eggs, while the **menstrual**

cycle governs the preparation and maintenance of the uterine lining ([\[link\]](#)). These cycles are coordinated over a 22–32 day cycle, with an average length of 28 days.

As with the male, the GnRH from the hypothalamus causes the release of the hormones FSH and LH from the anterior pituitary. In addition, **estrogen** and **progesterone** are released from the developing follicles. As with testosterone in males, estrogen is responsible for the secondary sexual characteristics of females. These include breast development, flaring of the hips, and a shorter period for bone growth.

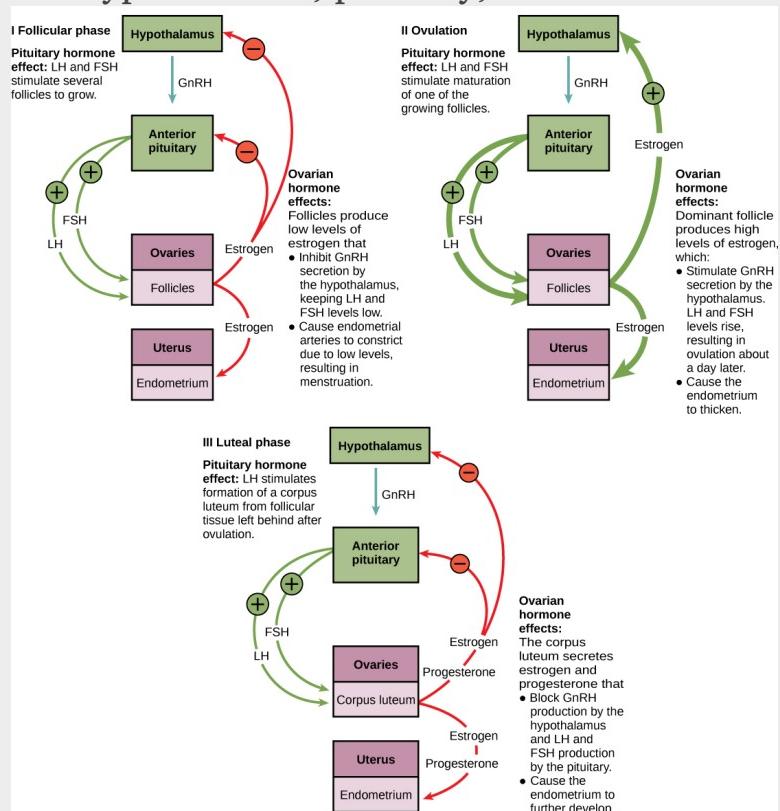
The Ovarian Cycle and the Menstrual Cycle

The ovarian and menstrual cycles are regulated by hormones of the hypothalamus, pituitary, and ovaries ([\[link\]](#)). The ebb and flow of the hormones causes the ovarian and menstrual cycles to advance. The ovarian and menstrual cycles occur concurrently. The first half of the ovarian cycle is the follicular phase. Slowly rising levels of FSH cause the growth of follicles on the surface of the ovary. This process prepares the egg for ovulation. As the follicles grow, they begin releasing estrogen. The first few days of this cycle coincide with menstruation or the sloughing off of the functional layer of the endometrium in the uterus. After about five days, estrogen levels rise and the menstrual

cycle enters the proliferative phase. The endometrium begins to regrow, replacing the blood vessels and glands that deteriorated during the end of the last cycle.

Visual Connection

The ovarian and menstrual cycles of female reproduction are regulated by hormones produced by the hypothalamus, pituitary, and ovaries.



Which of the following statements about hormone regulation of the female reproductive cycle is false?

1. LH and FSH are produced in the pituitary, and estrogen and progesterone are produced in the ovaries.
2. Estradiol and progesterone secreted from the corpus luteum cause the endometrium to thicken.
3. Both progesterone and estrogen are produced by the follicles.
4. Secretion of GnRH by the hypothalamus is inhibited by low levels of estrogen but stimulated by high levels of estrogen.

Just prior to the middle of the cycle (approximately day 14), the high level of estrogen causes FSH and especially LH to rise rapidly then fall. The spike in LH causes the most mature follicle to rupture and release its egg. This is **ovulation**. The follicles that did not rupture degenerate and their eggs are lost. The level of estrogen decreases when the extra follicles degenerate.

Following ovulation, the ovarian cycle enters its luteal phase and the menstrual cycle enters its secretory phase, both of which run from about day 15 to 28. The luteal and secretory phases refer to changes in the ruptured follicle. The cells in the follicle undergo physical changes and produce a structure called a corpus luteum. The corpus luteum produces estrogen and progesterone. The

progesterone facilitates the regrowth of the uterine lining and inhibits the release of further FSH and LH. The uterus is being prepared to accept a fertilized egg, should it occur during this cycle. The inhibition of FSH and LH prevents any further eggs and follicles from developing, while the progesterone is elevated. The level of estrogen produced by the corpus luteum increases to a steady level for the next few days.

If no fertilized egg is implanted into the uterus, the corpus luteum degenerates and the levels of estrogen and progesterone decrease. The endometrium begins to degenerate as the progesterone levels drop, initiating the next menstrual cycle. The decrease in progesterone also allows the hypothalamus to send GnRH to the anterior pituitary, releasing FSH and LH and starting the cycles again.

Career in Action

Reproductive Endocrinologist

A reproductive endocrinologist is a physician who treats a variety of hormonal disorders related to reproduction and infertility in both men and women. The disorders include menstrual problems, infertility, pregnancy loss, sexual dysfunction, and menopause. Doctors may use fertility drugs, surgery, or assisted reproductive techniques (ART)

in their therapy. ART involves the use of procedures to manipulate the egg or sperm to facilitate reproduction, such as *in vitro* fertilization. Reproductive endocrinologists undergo extensive medical training, first in a four-year residency in obstetrics and gynecology, then in a three-year fellowship in reproductive endocrinology. To be board certified in this area, the physician must pass written and oral exams in both areas.

(a) Fetal development is shown at nine weeks gestation. (b) This fetus is just entering the second trimester, when the placenta takes over more of the functions performed as the baby develops. (c) There is rapid fetal growth during the third trimester.
(credit a: modification of work by Ed Uthman; credit b: modification of work by National Museum of Health and Medicine; credit c: modification of work by Gray's Anatomy)

Gestation

Pregnancy begins with the fertilization of an egg and continues through to the birth of the individual. The length of time of **gestation**, or the **gestation period**, in humans is 266 days and is similar in other great apes.

Within 24 hours of fertilization, the egg nucleus has

finished meiosis and the egg and sperm nuclei fuse. With fusion, the cell is known as a zygote. The zygote initiates cleavage and the developing embryo travels through the oviduct to the uterus. The developing embryo must implant into the wall of the uterus within seven days, or it will deteriorate and die. The outer layers of the developing embryo or blastocyst grow into the endometrium by digesting the endometrial cells, and healing of the endometrium closes up the blastocyst into the tissue. Another layer of the blastocyst, the chorion, begins releasing a hormone called **human beta chorionic gonadotropin (β -HCG)**, which makes its way to the corpus luteum and keeps that structure active. This ensures adequate levels of progesterone that will maintain the endometrium of the uterus for the support of the developing embryo. Pregnancy tests determine the level of β -HCG in urine or serum. If the hormone is present, the test is positive.

The gestation period is divided into three equal periods or trimesters. During the first two-to-four weeks of the first trimester, nutrition and waste are handled by the endometrial lining through diffusion. As the trimester progresses, the outer layer of the embryo begins to merge with the endometrium, and the placenta forms. The **placenta** takes over the nutrient and waste requirements of the embryo and fetus, with the mother's blood passing nutrients to the placenta and removing waste from it. Chemicals from the fetus, such as bilirubin, are processed by

the mother's liver for elimination. Some of the mother's immunoglobulins will pass through the placenta, providing passive immunity against some potential infections.

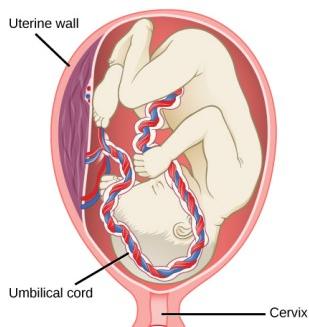
Internal organs and body structures begin to develop during the first trimester. By five weeks, limb buds, eyes, the heart, and liver have been basically formed. By eight weeks, the term fetus applies, and the body is essentially formed ([\[link\]a](#)). The individual is about five centimeters (two inches) in length and many of the organs, such as the lungs and liver, are not yet functioning. Exposure to any toxins is especially dangerous during the first trimester, as all of the body's organs and structures are going through initial development. Anything that interferes with chemical signaling during that development can have a severe effect on the fetus' survival.



(a)



(b)



(c)

During the second trimester, the fetus grows to about 30 cm (about 12 inches) ([\[link\]b](#)). It becomes active and the mother usually feels the first

movements. All organs and structures continue to develop. The placenta has taken over the functions of nutrition and waste elimination and the production of estrogen and progesterone from the corpus luteum, which has degenerated. The placenta will continue functioning up through the delivery of the baby. During the third trimester, the fetus grows to 3 to 4 kg (6.5–8.5 lbs.) and about 50 cm (19–20 inches) long ([\[link\]c](#)). This is the period of the most rapid growth during the pregnancy as all organ systems continue to grow and develop.

Concept in Action

Visit [this website](#) to see the stages of human fetal development.

Labor is the muscular contractions to expel the fetus and placenta from the uterus. Toward the end of the third trimester, estrogen causes receptors on the uterine wall to develop and bind the hormone oxytocin. At this time, the baby reorients, facing forward and down with the back or crown of the head engaging the cervix (uterine opening). This causes the cervix to stretch and nerve impulses are sent to the hypothalamus, which signals the release of oxytocin from the posterior pituitary. Oxytocin causes smooth muscle in the uterine wall to

contract. At the same time, the placenta releases prostaglandins into the uterus, increasing the contractions. A positive feedback relay occurs between the uterus, hypothalamus, and the posterior pituitary to assure an adequate supply of oxytocin. As more smooth muscle cells are recruited, the contractions increase in intensity and force.

There are three stages to labor. During stage one, the cervix thins and dilates. This is necessary for the baby and placenta to be expelled during birth. The cervix will eventually dilate to about 10 cm. During stage two, the baby is expelled from the uterus. The uterus contracts and the mother pushes as she compresses her abdominal muscles to aid the delivery. The last stage is the passage of the placenta after the baby has been born and the organ has completely disengaged from the uterine wall. If labor should stop before stage two is reached, synthetic oxytocin, known as Pitocin, can be administered to restart and maintain labor.

Section Summary

The reproductive structures that evolved in land animals allow males and females to mate, fertilize internally, and support the growth and development of offspring. Gametogenesis, the production of sperm (spermatogenesis) and eggs (oogenesis), takes place through the process of meiosis.

The male and female reproductive cycles are controlled by hormones released from the hypothalamus and anterior pituitary and hormones from reproductive tissues and organs. The hypothalamus monitors the need for FSH and LH production and release from the anterior pituitary. FSH and LH affect reproductive structures to cause the formation of sperm and the preparation of eggs for release and possible fertilization. In the male, FSH and LH stimulate Sertoli cells and interstitial cells of Leydig in the testes to facilitate sperm production. The Leydig cells produce testosterone, which also is responsible for the secondary sexual characteristics of males. In females, FSH and LH cause estrogen and progesterone to be produced. They regulate the female reproductive cycle, which is divided into the ovarian cycle and the menstrual cycle.

Human pregnancy begins with fertilization of an egg and proceeds through the three trimesters of gestation. The first trimester lays down the basic structures of the body, including the limb buds, heart, eyes, and the liver. The second trimester continues the development of all of the organs and systems. The third trimester exhibits the greatest growth of the fetus and culminates in labor and delivery. The labor process has three stages (contractions, delivery of the fetus, and expulsion of the placenta), each propelled by hormones.

Art Connections

[\[link\]](#) Which of the following statements about the male reproductive system is false?

1. The vas deferens carries sperm from the testes to the seminal vesicles.
 2. The ejaculatory duct joins the urethra.
 3. Both the prostate and the bulbourethral glands produce components of the semen.
 4. The prostate gland is located in the testes.
-

[\[link\]](#) D

[\[link\]](#) Which of the following statements about hormone regulation of the female reproductive cycle is false?

1. LH and FSH are produced in the pituitary, and estrogen and progesterone are produced in the ovaries.
2. Estradiol and progesterone secreted from the corpus luteum cause the endometrium to thicken.
3. Both progesterone and estrogen are produced by the follicles.
4. Secretion of GnRH by the hypothalamus is inhibited by low levels of estrogen but

stimulated by high levels of estrogen.

[link] C

Review Questions

Sperm are produced in the _____.

1. scrotum
 2. seminal vesicles
 3. seminiferous tubules
 4. prostate gland
-

C

Which female organ has an endometrial lining that will support a developing baby?

1. labia minora
 2. breast
 3. ovaries
 4. uterus
-

D

Which hormone causes FSH and LH to be released?

1. testosterone
 2. estrogen
 3. GnRH
 4. progesterone
-

C

Nutrient and waste requirements for the developing fetus are handled during the first few weeks by _____.

1. the placenta
 2. diffusion through the endometrium
 3. the chorion
 4. the blastocyst
-

B

Which hormone is primarily responsible for the contractions during labor?

1. oxytocin
2. estrogen
3. β -HCG
4. progesterone

A

Free Response

Compare spermatogenesis and oogenesis as to timing of the processes, and the number and type of cells finally produced.

Stem cells are laid down in the male during gestation and lie dormant until adolescence. Stem cells in the female increase to one to two million and enter the first meiotic division and are arrested in prophase. At adolescence, spermatogenesis begins and continues until death, producing the maximum number of sperm with each meiotic division. Oogenesis continues again at adolescence in batches of eggs with each menstrual cycle. These primary oocytes finish the first meiotic division, producing a viable egg with most of the cytoplasm and its contents, and a second cell called a polar body containing 23 chromosomes. The second meiotic division is initiated and arrested in metaphase. At ovulation, one egg is released. If this egg is fertilized, it finishes the second meiotic division. This is a diploid, fertilized egg.

Describe the events in the ovarian cycle leading up to ovulation.

Low levels of progesterone allow the hypothalamus to send GnRH to the anterior pituitary and cause the release of FSH and LH. FSH stimulates follicles on the ovary to grow and prepare the eggs for ovulation. As the follicles increase in size, they begin to release estrogen and a low level of progesterone into the blood. The level of estrogen rises to a peak, causing a spike in the concentration of LH. This causes the most mature follicle to rupture and ovulation occurs.

Describe the stages of labor.

Stage one of labor results in uterine contractions, which thin the cervix and dilate the cervical opening. Stage two delivers the baby, and stage three delivers the placenta.

Glossary

bulbourethral gland

the paired glands in the human male that

produce a secretion that cleanses the urethra prior to ejaculation

corpus luteum

the endocrine tissue that develops from an ovarian follicle after ovulation; secretes progesterone and estrogen during pregnancy

clitoris

a sensory and erectile structure in female mammals, homologous to the male penis, stimulated during sexual arousal

estrogen

a reproductive hormone in females that assists in endometrial regrowth, ovulation, and calcium absorption

follicle stimulating hormone (FSH)

a reproductive hormone that causes sperm production in men and follicle development in women

gestation

the development before birth of a viviparous animal

gestation period

the length of time of development, from conception to birth, of the young of a viviparous animal

gonadotropin-releasing hormone (GnRH)

a hormone from the hypothalamus that causes the release of FSH and LH from the anterior pituitary

human beta chorionic gonadotropin (β -HCG)

a hormone produced by the chorion of the zygote that helps to maintain the corpus luteum and elevated levels of progesterone

inhibin

a hormone made by Sertoli cells, provides negative feedback to hypothalamus in control of FSH and GnRH release

interstitial cell of Leydig

a cell type found next to the seminiferous tubules that makes testosterone

labia majora

the large folds of tissue covering inguinal area

labia minora

the smaller folds of tissue within labia majora

luteinizing hormone (LH)

a reproductive hormone in both men and women, causes testosterone production in men and ovulation and lactation in women

menstrual cycle

the cycle of the degradation and re-growth of

the endometrium

oogenesis

the process of producing haploid eggs

ovarian cycle

the cycle of preparation of egg for ovulation
and the conversion of the follicle to the
corpus luteum

oviduct

(also, fallopian tube) the muscular tube
connecting uterus with ovary area

ovulation

the release of an oocyte from a mature follicle
in the ovary of a vertebrate

penis

the male reproductive structure for urine
elimination and copulation

placenta

the organ that supports the transport of
nutrients and waste between the mothers and
fetus' blood in eutherian mammals

progesterone

a reproductive hormone in women; assists in
endometrial regrowth and inhibition of FSH
and LH release

prostate gland

a structure that is a mixture of smooth muscle and glandular material and that contributes to semen

scrotum

a sac containing testes, exterior to body

semen

a fluid mixture of sperm and supporting materials

seminal vesicle

a secretory accessory gland in male; contributes to semen

seminiferous tubule

the structures within which sperm production occurs in the testes

Sertoli cell

a cell in the walls of the seminiferous tubules that assists developing sperm and secretes inhibin

spermatogenesis

the process of producing haploid sperm

testes

a pair of male reproductive organs

testosterone

a reproductive hormone in men that assists in sperm production and promoting secondary

sexual characteristics

uterus

a female reproductive structure in which an embryo develops

vagina

a muscular tube for the passage of menstrual flow, copulation, and birth of offspring